Nota Lepi. **43** 2020: 181–210 | DOI 10.3897/nl.43.49512 Research Article

Morphological evolution in *Hyles* Hübner, 1819 hawkmoths (Lepidoptera, Sphingidae): reconstructing the ancestral *Hyles* habitus

Anna K. Hundsdoerfer[1], Ian J. Kitching[2]

1 *Molecular Laboratory, Museum of Zoology, Senckenberg Natural History Collections Dresden, Königsbrücker Landstrasse 159, 01109 Dresden, Germany*

2 *Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK*

http://zoobank.org/03AE03E9-30F1-47CC-9481-9300D9450AB5

Received 18 December 2019; accepted 14 April 2020; published: 31 July 2020
Subject Editor: Lauri Kaila.

Abstract. Molecular phylogenetic studies suggest that similar wing and body patterns in the hawkmoth genus *Hyles* Hübner, [1819] do not necessarily reflect a close phylogenetic relationship. To improve our understanding of morphological evolution in these organisms, 75 characters derived from the external adult morphology are explicitly coded and analysed in a maximum parsimony cladistic framework. The results corroborate the hypothesis that wing and body patterns have indeed reappeared in different parts of the phylogeny but the underlying genetic mechanism remains to be determined. By reconstructing the suite of ancestral states of the morphological characters using Bayesian inference, we derived an approximation of the appearance of the proto-*Hyles* species. The overall habitus of this moth does not display a combination of characters found in any extant *Hyles* species. Rather, the forewings are most like those of members of the *Hyles euphorbiae*-complex but with better developed antemedial and postmedial lines, the hindwings are typical *Hyles*, and the abdominal pattern most closely resembles that of *Hyles euphorbiarum* (Guérin-Méneville & Percheron, 1835), but with one fewer pairs of black subdorsal patches. Within the context of the subtribe Choerocampina and Sphingidae more generally, the proto-*Hyles* reconstruction does not resemble any other species apart from *Rhodafra opheltes* (Cramer, 1780), but this appears to be another instance of convergent pattern expression.

Introduction

Molecular phylogenetic studies of the genus *Hyles* Hübner, [1819] (Lepidoptera: Sphingidae) have led to the realisation that similar wing and body patterns in this genus do not necessarily reflect a close phylogenetic relationship (Hundsdoerfer et al. 2005, 2009, 2017). The most striking example of this disparity is provided by the four species, *H. lineata* (Fabricius, 1775) (Nearctic and Neotropical), *H. livornica* (Esper, 1780) (Afro-Palaearctic), *H. tatsienluica* (Oberthür, 1916) (Tibetan Plateau) and *H. livornicoides* (Lucas, 1892) (Australia). All four have superficially similar forewing upperside patterns, in which the olive green-brown costal and postmedial regions are separated by a narrow and approximately parallel-sided oblique cream band, and the veins are all strongly highlighted in white. In addition, the upperside of the abdomen has more than three pairs of subdorsal black spots (except *H. livornicoides*) and the median white line has a row of small black spots on either side, one per segment. As a consequence, the four species have been considered to be closely related, with both *H. livornicoides* and *H. livornica* sometimes being treated as subspecies of *H. lineata* (Rothschild and Jordan 1903) and *H. tatsienluica* as a junior synonym of *H. livornica* (Kitching and Cadiou 2000); they have even been placed in their own subgenus,

Danneria Eitschberger & Zolotuhin, 1998 (Danner et al. 1998). However, all molecular phylogenetic hypotheses (Hundsdoerfer et al. 2005, 2009, 2017) have consistently placed *H. lineata* as the sister group to all other *Hyles* with full support. The placement of *Hyles livornicoides* as sister to the Madagascan *H. biguttata* (Walker, 1856) was not as well supported (65% bootstrap (bs) support in the preferred total evidence tree in Hundsdoerfer et al. 2009: fig. 3, and 0.72 Bayesian posterior probability (pp) and bs below 50% in Hundsdoerfer et al. 2017: fig. 2) but no analysis proposed a close relationship with either *H. lineata* or *H. livornica*, This latter species, together with its Tibetan endemic sister taxon, *H. tatsienluica*, groups within the Palearctic *Hyles* clade. Based on the well-supported basalmost position of *H. lineata*, we hypothesize that its wing pattern is ancestral (plesiomorphic) within the genus. Its subsequent independent appearance in two more distal groups of *Hyles* (*H. livornica/tatsienluica* and *H. livornicoides*), after having been modified in intervening lineages, would then have to be ascribed to an unknown genetic mechanism or, alternatively, the pattern may have arisen three times independently. In the main alternative pattern, the costal olive green-brown band of the forewing upperside is partially or completely broken up into spots and patches and the veins are never highlighted in white (although they may be highlighted in the beige ground colour, see below), and the upperside of the abdomen has no more than three pairs of subdorsal black spots and the median white line has no small black spots on either side. *Hyles nicaea* (von Prunner, 1798) (Palaearctic), shows this in its clearest and most contrasting form, but it also occurs, with varying degrees of differentiation, in *H. annei* (Guérin-Méneville, 1839) (South America), *H. biguttata* (Madagascar), *H. calida* (Butler, 1881) (Hawaii), *H. euphorbiae* (Linnaeus, 1758) (Holarctic) and the Central Asian *H. centralasiae* (Staudinger, 1887), *H. salangensis* (Ebert, 1969) and *H. stroehlei* Eitschberger, Danner & Surholt, 1998.

As in other groups of hawkmoths, *Hyles* moths from arid regions are often paler, with less contrasting and more homogeneous wing markings. Breeding experiments in which siblings were reared at different temperatures (de Freina 1994) have confirmed that this variation in the intensity of the dark patterning is influenced by environmental temperature. Despite this, the two main patterns described above can be easily discerned, with one exception: the patterns in some *H. tithymali* (Boisduval, 1834) and *H. livornica* from Northern Africa can converge in some individuals as the result of strong fading caused by high incident light levels in the environments in which these moths live.

However, to date no study has explicitly coded external *Hyles* morphology and analysed the data in a cladistic framework to increase the understanding of morphological evolution in these insects.

The present paper has three aims: 1) to investigate in detail the morphological variation within *Hyles* by explicitly coding a suite of morphological characters (including representatives of several other Choerocampina genera as outgroups), then analysing these data using maximum parsimony methods; 2) to compare the results with the relationships postulated from the analyses of molecular data; and 3) to reconstruct the ancestral state suite of the morphological characters and thus the appearance of the proto-*Hyles* species.

Material and methods

The study included 218 individuals of Choerocampina, an ingroup comprising 193 samples of *Hyles* species and subspecies and 25 outgroup samples from other genera. The identification and the taxonomy follow Kitching (2019) (publication of the more recent paper by Hundsdoerfer, Lee et al. 2019 unfortunately overlapped the production of the present paper and their synonymy of five species of the *Hyles euphorbiae* complex (HEC) could not be readily implemented). Specimens of

two species of *Hyles*, *Hyles costata* (von Nordmann, 1851) and *Hyles svetlana* Shovkoon, 2010, were unavailable for study. Where possible, we examined at least five specimens of each species and three of each subspecies (if there was more than one). The holotype and paratype of *H. churkini* Saldaitis & Ivinskis, 2006 and the specimens in the research collection of P. Smetacek were scored from colour photographs.

Data for 75 anatomical characters were obtained from the head (4), legs (3), thorax (6), abdomen (16); forewing pattern (40) and hindwing pattern (6). Character definitions, descriptions and explanations of character states are provided in Appendix I. Observations of pinned adults were made under a stereomicroscope. Selected characters are illustrated in Figures 1–9 as follows, based on specimens from the Lepidoptera collection of the SNSD: head (dorsal antennal scaling, Fig. 1; scaling in labial palp segments 1 and 2, Figs 2, 3); legs (arolium, Fig. 4; foreleg basitarsus spines, Fig. 5); thorax and abdomen (scaling, Figs 6, 7); and fore- and hindwing (pattern elements, Figs 8, 9). Other characters, especially colour characters, are illustrated by means of active linked cross-references to the URLs of species pages on the Sphingidae Taxonomic Inventory (Kitching 2019), where relevant colour images can be found under the Media tab. Anatomical terminology in the character descriptions and associated information (Appendix I) follows Kitching and Cadiou (2000).

The data set of character states for the 218 individuals is presented in Suppl. material 1: Table S1; locality and other label data is provided in Suppl. material 2: Table S2. Character delimitations and coding follow the methods proposed by Sereno (2007), who provided strong and logical arguments for separating neomorphic and transformational characters by means of contingent coding (Forey and Kitching 2000). Multistate transformational characters were treated as unordered. Missing data are indicated by a question mark (?). Characters that could not be scored due to absence of homologous structures (dependent characters) are indicated by a dash (-). Polymorphic characters are explicitly coded as exhibiting only those states observed. The abbreviation ch. (plural = chs) is used to denote the word character.

Specimens from the following collections were examined during the study: Natural History Museum, London, UK (NHMUK; n = 191); Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden, Germany (SNSD; n = 7); Naturhistorisches Museum Wien, Austria (NHMW; n = 6); and the Thomas Witt Museum, München, Germany (MTWM; n = 5); and the research collection of P. Smetacek, Jones Estate, Bhimtal, Nainital, Uttarakhand, India (n = 9).

Analyses

Maximum parsimony analyses were implemented using WinClada version 1.00.08 (Nixon 1999–2002) (equal weighting, EW) and TNT version 1.1 (Willi Hennig Society Edition, viii.2011) (Goloboff et al. 2008) (implied weighting, IW). Five separate runs under EW were undertaken using the Parsimony Ratchet, each with 5000 iterations per replicate and holding 10 trees per iteration. The results of all five runs were then concatenated and the groups common to all the most parsimonious cladograms (MPCs) summarized by means of a strict consensus tree (SCT) and a majority rule consensus tree (MRCT). IW analysis was undertaken using the New Technology options of TNT: sectorial searches, ratchet, tree drifting and tree fusing. For the ratchet, the up/downweighting probabilities were set to 5% and the number of replicates to 200. The number of cycles of tree drifting was set to 50. All other search parameters remained at their default settings. Analyses were terminated once the MPC had been found 10 times. The maximum number of trees held was set to 10,000. Following preliminary analyses (not shown), the value of the concavity constant, K, which determines the strength of the weighting against homoplastic characters, was

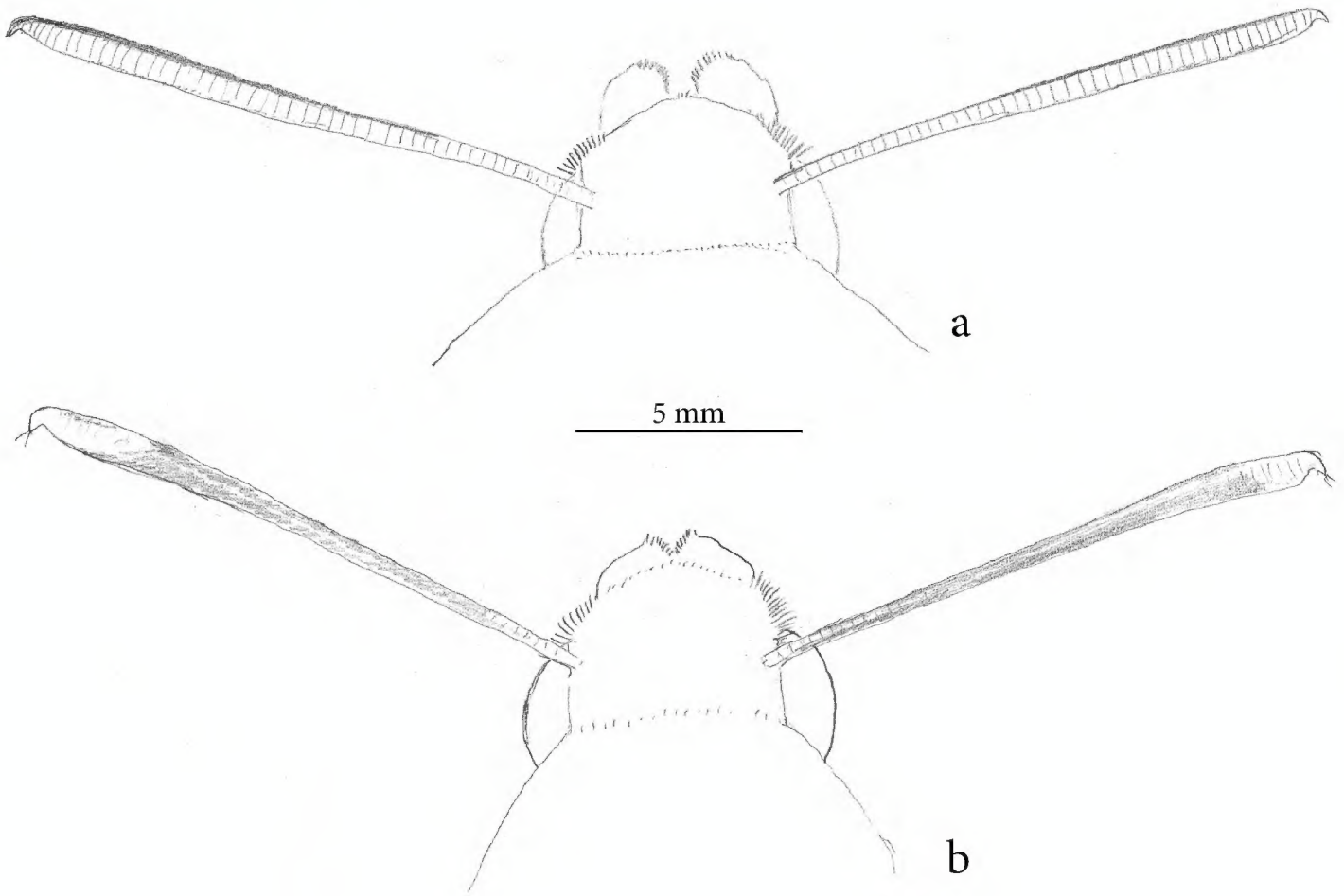

Figure 1. Head (dorsal view) of (**a**) *Hyles euphorbiae* (Germany, Dresden, coll. Barkowski, MTD, same individual as Fig. 9c) and (**b**) *H. livornica* (Italy, Cuma-Campania, dune area, leg. R. Remane, MTD, same individual as Figs 5c, 6f, 9b).

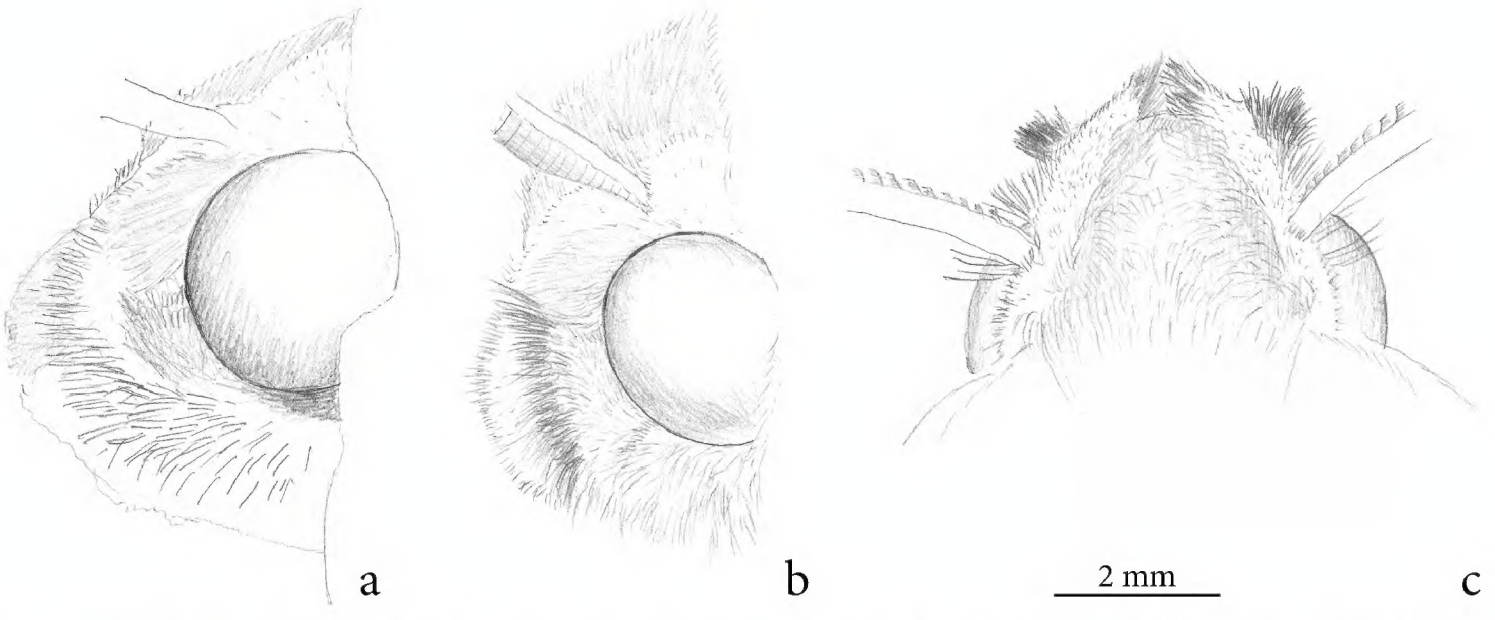

Figure 2. Head of (**a**) *Hyles gallii* (lateral view; near Zeughaus, Saxon Switzerland, Germany, MTD), (**b**) lateral view and (**c**) dorsal view of *Rhodafra opheltes* (Natal, R.S.A., BMNH(E) 1325540).

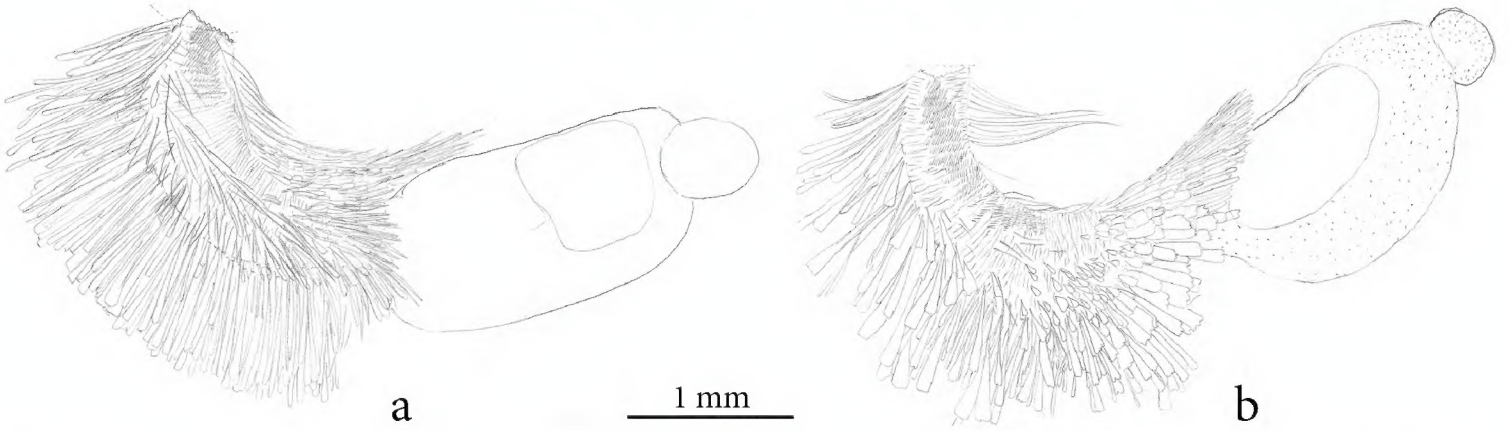

Figure 3. Inner side of left labial palp of (**a**) *Hyles euphorbiae* (no data, MTD) and (**b**) *Theretra oldenlandiae* (no data, MTD).

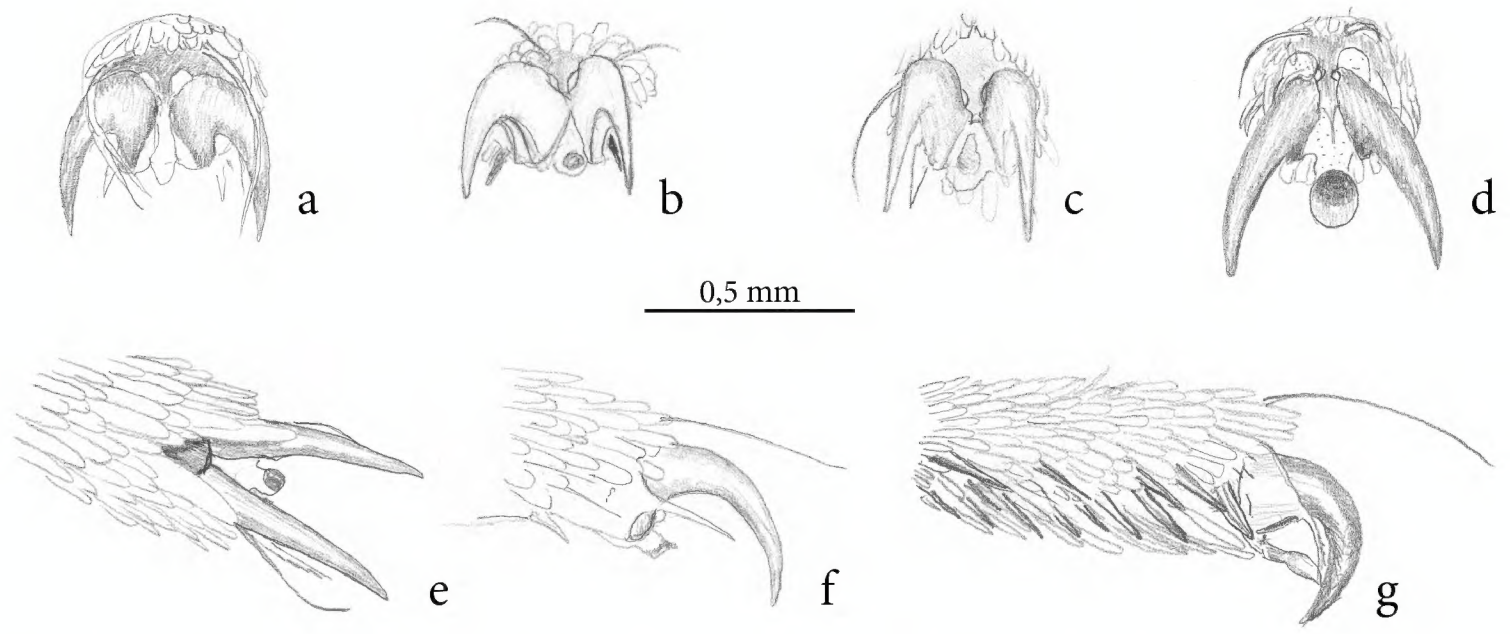

Figure 4. Foreleg tarsus of (**a**) *Hyles hippophaes* (no date, MTD), (**b**, **c**, **e**, **f**) *H. vespertilio* (Switzerland, Genf, coll. P. Denso, MTD) same individual as Figs 6a, 9f), (**d**, **g**) *H. gallii* (Sweden, MTD-TW4049). (**a–d**, apical view, **e**, dorsal view; **f**, **g**, lateral view).

set to 16. Cladograms were prepared using WinClada ver. 1.00.08 and rooted between *Hippotion celerio* (Linnaeus, 1758) and the remaining taxa.

Reconstruction of ancestral body and wing pattern of *Hyles*

To reconstruct the ancestral *Hyles* wing pattern, we reanalysed the slightly augmented dataset used in the ancestral state analysis in Hundsdoerfer et al. (2017; concatenated COI, COII and EF1α sequences; but with three intraspecific groupings added within *H. gallii* (Rottemburg, 1775), *H. hippophaes* (Esper, 1789) and *H. nicaea*, to make a 25 taxon-set rather than 22) to yield a Bayesian reconstruction total evidence tree using MrBayes 3.2 (Ronquist et al. 2012). The taxa were chosen to represent each of the clades and no sequence data were available for *H. wilsoni* (Rothschild, 1894), *H. n. nicaea*, *H. n. orientalis* (Austaut, 1905), *H. apocyni* (Shchetkin, 1956), *H. chamyla* (Denso, 1913), *H. nervosa* (Rothschild & Jordan, 1903), *H. churkini* or *H. exilis* Der-

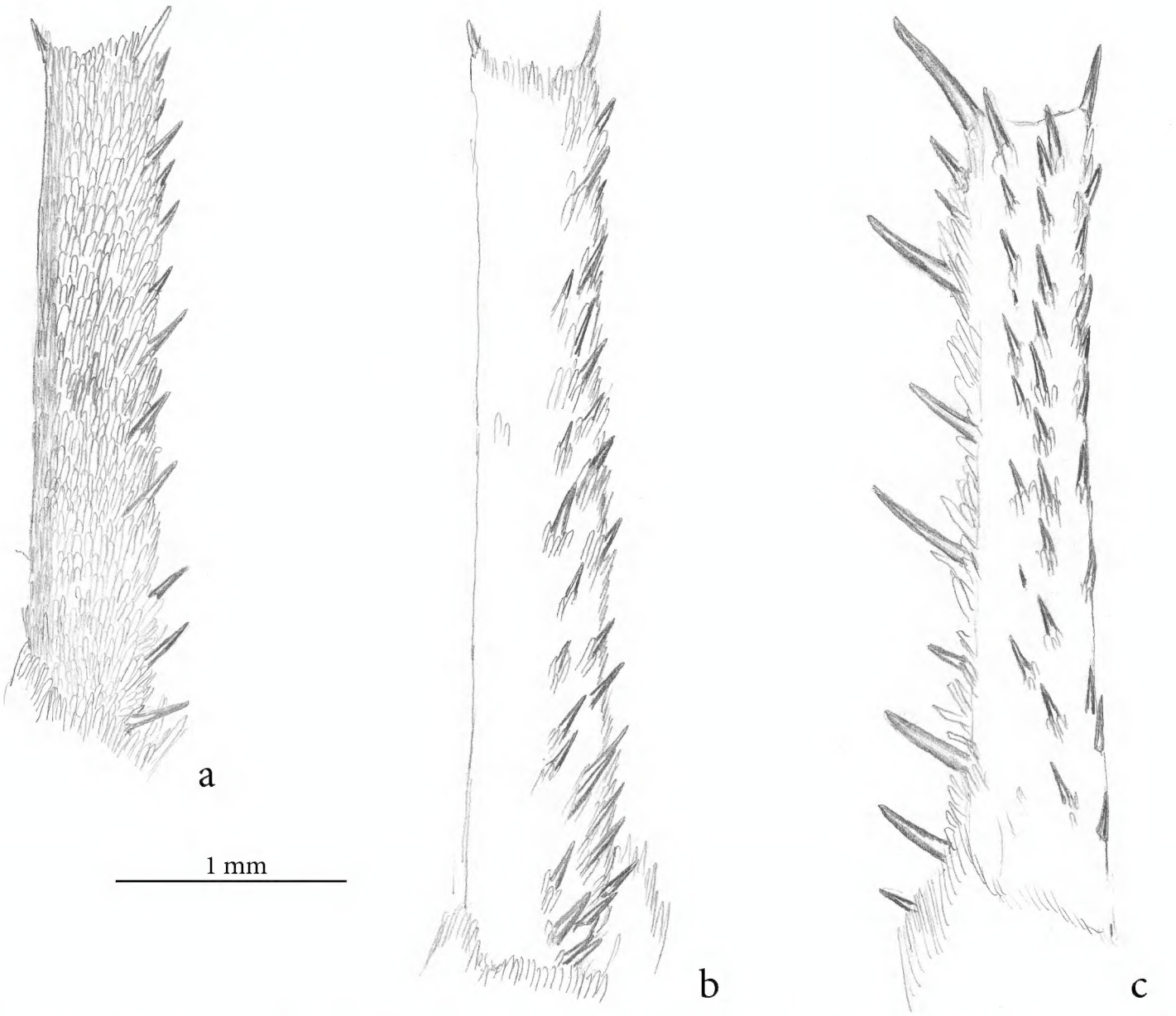

Figure 5. Foreleg basitarsus of (**a**) *Hyles tithymali* (no data, MTD), (**b**) *H. nicaea castissima* (Austaut, 1883) (Algeria, Tlemcen, MTD), (**c**) *H. livornica* (Italy, same individual as Figs 1b, 6f, 9b).

zhavets, 1979 (formerly *H. chuvilini* Eitschberger, Danner & Surholt, 1998). The morphological matrix was then condensed to the same OTU set by reducing the number of taxa and collapsing the character states of the individuals to one per taxon (Suppl. material 3: Table S3). Intraspecific variation was coded as explicit polymorphic character states. After excluding the burnin of 25% from the Bayesian reconstruction, 26310 trees were submitted to Mesquite (v. 2.75 build 564; Maddison and Maddison 2014) for the maximum likelihood ancestral state reconstruction of the morphological character states. The result of this analysis is shown as an additional line of character states in the matrix of 75 characters (Suppl. material 3: Table S3). The appearance of Proto-*Hyles* was then deduced from this result and the character states rendered and illustrated in the same way as was used to produce the drawings of the character states for the descriptions of characters (Figs 1–7, 9). Aspects of the appearance that were not coded in the character list were completed by the artist with reference to the specimens used to produce the drawings of the *Hyles* specimens. These features included habitus characters, such as the general shapes and relative sizes of the thorax, abdomen and wings, and elements thereof (e.g., eyes, patagia, tegulae). The general aspect of Proto-*Hyles* should thus not be interpreted as full reconstruction.

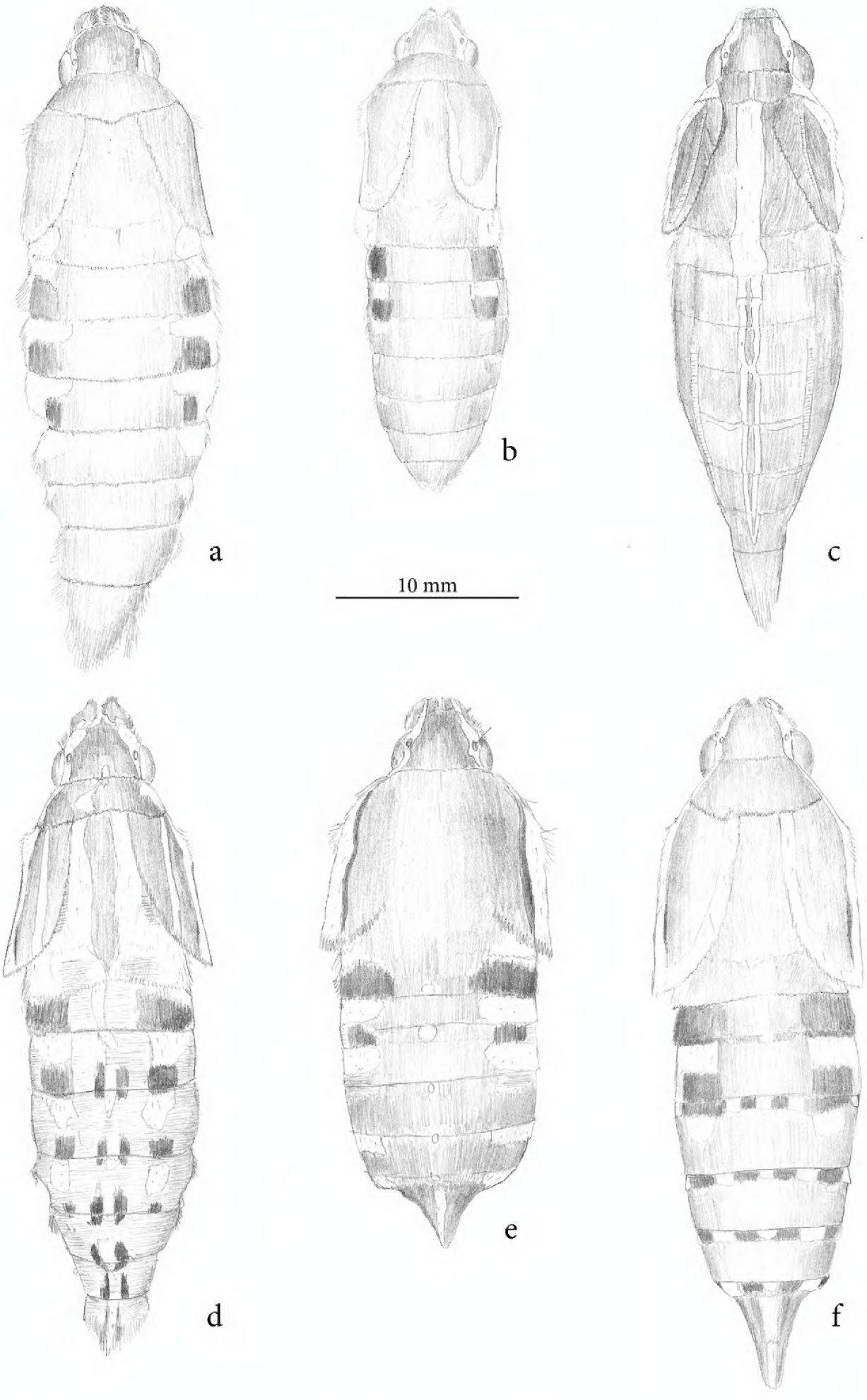

Figure 6. Bodies (without wings, antennae) of (**a**) *Hyles vespertilio* (Switzerland, same individual as Figs 4b, c, e, f, 6a, 9f), (**b**) *H. zygophylli* (Russia, Sarepta, coll. Staudinger and Bang-Haas, MTD; same individual as Fig. 9i), (**c**) *Theretra oldenlandiae* (Fabricius, 1775) (no data, MTD), (**d**) *H. lineata* (U.S.A., New Jersey, leg. Ernst, MTD), (**e**) *H. gallii* (Germany, Saxon Switzerland, MTD), (**f**) *H. livornica* (Italy, same individual as Figs 1b, 5c, 9b).

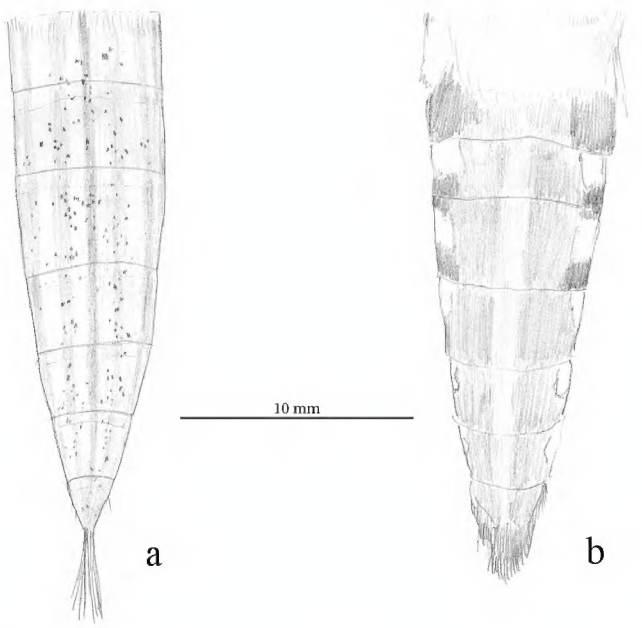

Figure 7. Abdomen segments 2–8 of (**a**) *Xylophanes loelia* (Druce, 1878) (Brazil?, Para, leg. S. Wähner, MTD), (**b**) *Hyles euphorbiarum* (Chile, MTD).

Results

Analysis of the 75 morphological characters (Suppl. material 1: Table S1) under EW yielded 82166 most parsimonious cladograms (MPCs) of length 432 steps, consistency index (CI) = 0.19 and retention index (RI) = 0.86. The strict consensus tree (SCT) of these MPCs (Suppl. material 4: Fig. S1a) collapses 162 nodes and is highly unresolved. Most nodes within *Hyles* collapse into a very large clade that also includes *Chaerocina* Rothschild & Jordan, 1903, *Deilephila* [Laspeyres], 1809 and *Rhodafra* Rothschild & Jordan, 1903, only the first of which is recovered as monophyletic. Although there are known, albeit not widely acknowledged, theoretical and methodological issues regarding the implementation and interpretation of MRCTs (Sharkey and Leathers 2001), they are nevertheless useful in exploring possible phylogenetic relationships, providing they are interpreted with care. The MRCT derived from the 82166 MPCs found under EW (Suppl. material 4: Fig. S1b) is, as expected, much more resolved than the SCT. Most of the outgroup species are now placed outside of *Hyles* but only three of the six genera in which more than one species was coded are recovered as monophyletic (*Basiothia* Walker, 1856, *Xylophanes* Hübner, [1819], *Chaerocina*). *Deilephila* and *Rhodafra* are both recovered as polyphyletic and *Hyles* is only monophyletic if the two species *D. elpenor* (Linnaeus, 1758) and *R. opheltes* (Cramer, 1780) are included.

Within *Hyles*, both EW consensus trees (Suppl. material 4: Fig. S1a, b) include a clade comprising the three Hawaiian species studied, all of which are monophyletic, and with *H. calida* placed as sister to *H. perkinsi* (Swezey, 1920) + *H. wilsoni*. In the MRCT (Suppl. material 4: Fig. S1b), this clade is first to branch off within *Hyles*, followed by *H. vespertilio* (Esper, 1780), *H. salangensis* and then a large clade of species characterized by forewings with little pattern contrast (*H. apocyni*, *H. centralasiae*, *H. chamyla*, *H. hippophaes*, and *H. siehei* (Püngeler, 1903)). Only one of these species in this last group, *H. siehei*, is recovered as monophyletic. All these groups can be characterized as having forewing patterns that lack many or most of the elements found in the crown group, which comprises two clades. The first consists of moths with a large proportion of darker areas on the forewings (monophyletic *H. lineata*, *H. gallii* and *H. euphorbiarum* (Guérin-Méneville & Percheron, 1835), *H. livornica* (including the sole sample of *H. tatsienluica*),

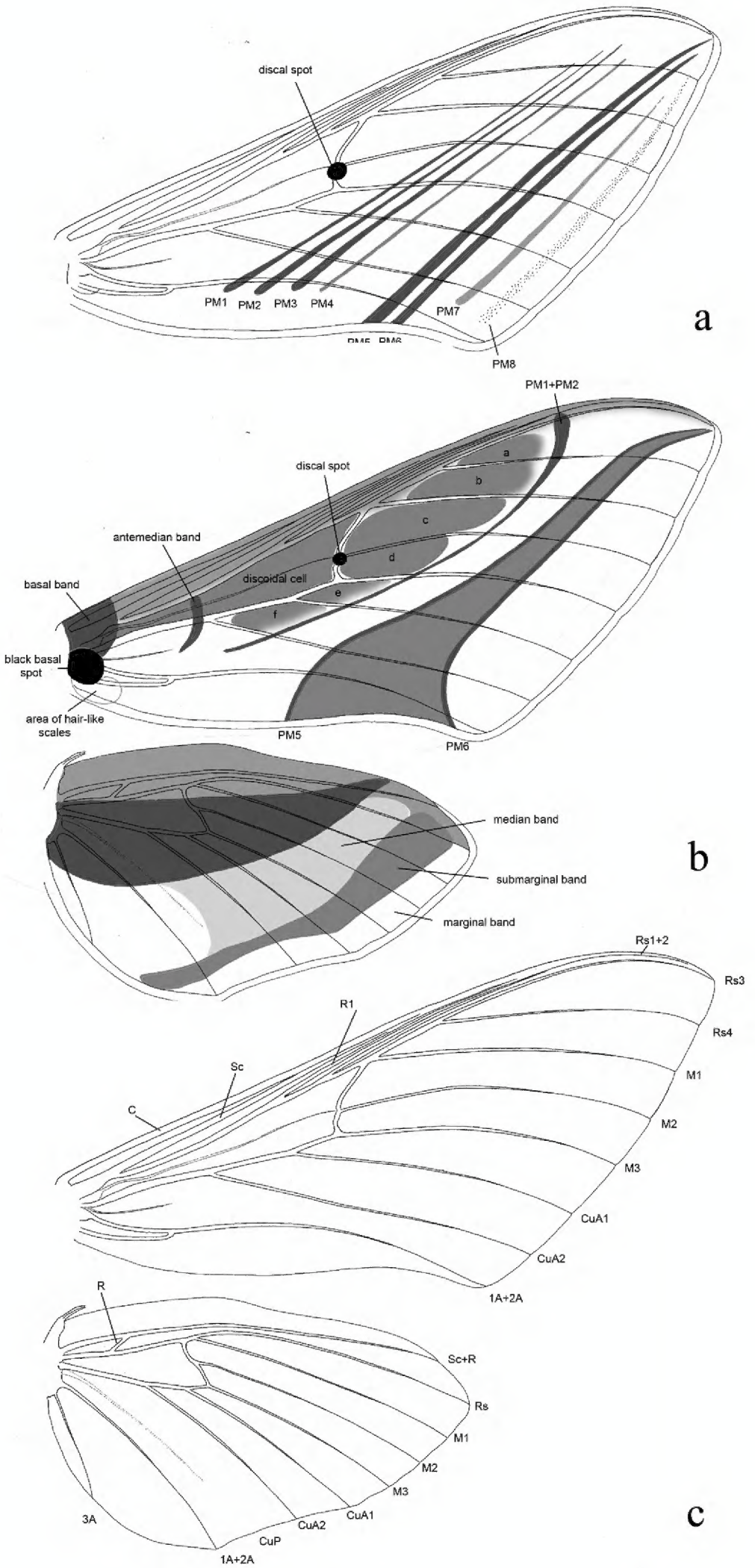

Figure 8. Schematic representations of wings in Choerocampina. (**a**) Forewing ground pattern (not *Hyles*), (**b**, **c**) fore- and hindwings with (**b**) *Hyles* pattern elements and (**c**) wing venation labels.

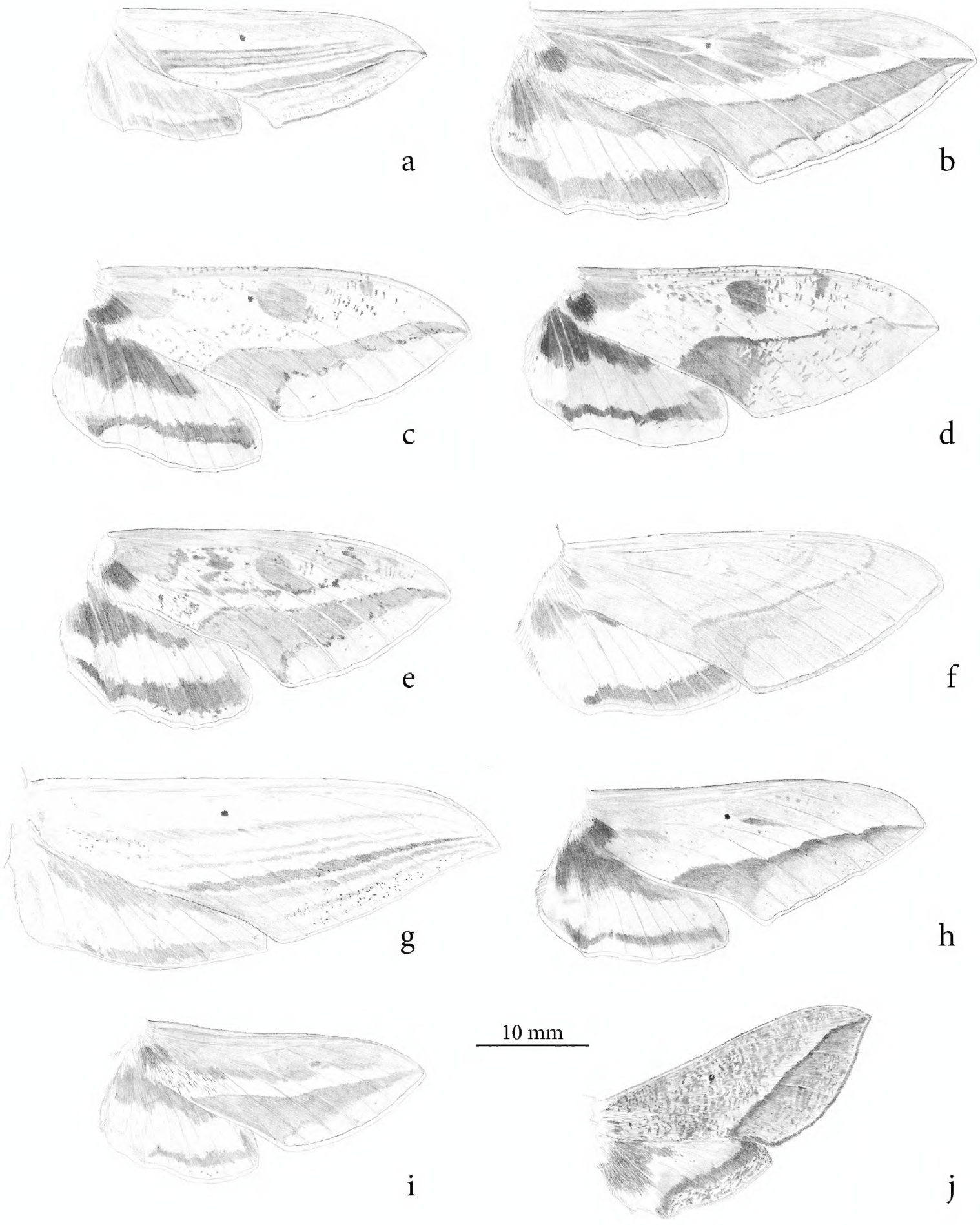

Figure 9. Wings (right side) of (**a**) *Theretra oldenlandiae* (no data, MTD), (**b**) *Hyles livornica* (Italy, same individual as Figs 1b, 5c, 6f), (**c**) *H. euphorbiae* (Germany, same individual as Fig. 1a), (**d**) *H. nicaea orientalis* (Krim, ex coll. A. Brehm, coll. Kleinschmidt/Wittenberg, MTD), (**e**) *H. dahlii* (Corsica, coll. Ernst, MTD), (**f**) *H. vespertilio*, Switzerland, same individual as Figs 4b, c, e, f, 6a, 9f), (**g**) *Xylophanes loelia* (S. Pablo de Olivenca, Ob. Amazonas, leg. S. Waehner, MTD), (**h**) *H. hippophaes* (no data, coll. W. Henitz), (**i**) *H. zygophylli* (Russia, same individual as Fig. 6b), (**j**) *Rhodafra marshalli* (Zambia, BMNH(E) 1325537).

paraphyletic *H. zygophyllii* (Ochsenheimer, 1808) and *H. livornicoides*, the similar-looking *R. opheltes*, and *Deilephila elpenor*. The second clade is dominated by the HEC s.l. and three species that have broadly similar forewing patterns, *H. nicaea*, *H. annei* and *H. biguttata*, of which the last two form a reciprocally monophyletic pair of sister species. *Hyles dahlii* (Geyer [1828]), *H. churkini* (only two individuals), *H. exilis* and *H. nicaea* are also recovered as monophyletic, whereas *H. nervosa*, *H. stroehlei* and the remaining members of the HEC s.s. (the former *H. cretica* Eitschberger, Danner & Surholt, 1998, *H. euphorbiae*, *H. robertsi* (Butler, 1880), *H. sammuti* Eitschberger, Danner & Surholt, 1998, *H. tithymali*) are not.

Analysis of the morphological data set (Suppl. material 1: Table S1) under IW ($K = 16$) yielded 37 MPCs of fit = 13.71749, length 444 steps, CI = 0.18 and RI = 0.86. The SCT of these MPCs (Suppl. material 5: Fig. S2) collapses 107 nodes with most of the loss of resolution occurring in clades comprising samples of the same species or subspecies, the main exception being the taxa of the HEC. The MRCT of the 37 IW MPCs (not shown) is only slightly more resolved, mostly among samples of individual species. Under IW (Suppl. material 5: Fig. S2), *Deilephila* is recovered as the paraphyletic sister group comprising *Hyles* and *Rhodafra*. This latter genus is monophyletic, as are its two component species, but it is nested deep inside *Hyles*, where it is placed as sister to *H. gallii*, with this group being sister to *H. euphorbiarum*. As in the EW MRCT (Suppl. material 4: Fig. S1b), first to branch off within *Hyles* under IW (Suppl. material 5: Fig. S2) is the clade of Hawaiian endemics (see above), followed again by *H. vespertilio* then *H. salangensis*. Beyond that, however, the pattern is confused by the apparently scattered placement of various members of the HEC, many of which are placed in paraphyletic arrangements at the bases of clades comprising other species. Thus, the next node is a nine-way polytomy consisting of 10 HEC (four singletons and two groups of three), the *H. centralasiae-H. hippophaes* clade noted above in the EW MRCT (Fig. 1b), a clade comprising *H. annei* + *H. biguttata* placed as sister to a monophyletic *H. nicaea*, and a large clade that includes all the other *Hyles* individuals plus *Rhodafra*. Within this last clade, the lowest branches consist of several HEC members, followed by two large clades. The first includes the bulk of the remaining HEC s.s. individuals and a terminal clade consisting of *Hyles dahlii* + *H. nervosa* placed as sister to *H. exilis*. At the base of the second large clade are two further HEC individuals followed by *H. churkini* and a paraphyletic *H. zygophylli*. These are followed by a clade comprising the four members of the former subgenus *Danneria* (see Introduction), in which a monophyletic *H. lineata* is sister to a monophyletic *H. livornicoides*, and these in turn are sister to *H. livornica*, including the single individual of *H. tatsienluica*. Finally, there is a terminal clade in which the genus *Rhodafra* (with its two reciprocally monophyletic species) is sister to *H. gallii*, and these two are sister to *H. euphorbiarum*.

Ancestral wing pattern of *Hyles*

For 64 of the 75 characters, the maximum likelihood ancestral state reconstruction analysis yielded an unequivocal ancestral state assignment. For the remaining 11 characters with equivocal states, the state with the largest unequivocal state percentage was chosen to be represented in the reconstruction and the alternatives disregarded. The reconstruction of the ancestral states of the morphological characters within *Hyles*, illustrated as the habitus of a proto-*Hyles* moth (Fig. 10), does not display an overall combination of characters found in any outgroup or extant *Hyles* species. Rather, it shows an abdominal pattern similar to that of the two South American species (e.g., more than three black spots) combined with a forewing pattern resembling members of the HEC.

Discussion

A major challenge in this study was to disentangle the complex homologies of the wing and abdominal pattern elements. However, as many of the relationships represented in the consensus trees based on morphological characters reflect external similarity and sometimes former taxonomy, we appear to have interpreted these homologies correctly. For example, *H. tatsienluica* is placed within *H. livornica* and subgenus *Danneria* is consistently recovered as monophyletic (Suppl. material 4: Figs S1 and Suppl. material 5: Fig. S2). Furthermore, in the EW MRCT (Suppl. material 4: Fig. S1b) (but not the IW SCT, Suppl. material 5: Fig. S2), *H. nicaea* is within the HEC, consistent with the subgenus *Hyles* as interpreted by Danner et al. 1998). However, as expected from the pioneering molecular phylogenetic studies of Hundsdoerfer et al. (2005, 2009), the results of our morphological analyses are in conflict with the phylogenetic hypotheses supported by the molecular data. The EW analysis in particular is dominated by forewing pattern element characters, many of which *Rhodafra opheltes* shares with species of *Hyles*, especially with *H. euphorbiarum*. Thus, it is unsurprising to find this *Rhodafra* species nested deep within *Hyles*, in a group that also includes *Hyles gallii* and *Deilephila elpenor*. In stark contrast, the highly simplified forewing pattern of *R. marshalli*, which lacks most of the elements seen in *R. opheltes* and *Hyles*, results in this species branching off very close to the base of the tree (Suppl. material 4: Fig. S1b). Under IW, however, the characters of the labial palp lateral hairs (chs 2 & 3) are given high weight, resulting in a monophyletic *Rhodafra*, sister to *Hyles gallii* (Fig. 2). This is a similar result to the molecular phylogeny based on maximum likelihood (ML) analyses of mitochondrial data found by Hundsdoerfer and Kitching (in press: figs 1, 2). In contrast, in the same study, analysis of EF1α nuclear sequence data using ML placed *Rhodafra* as sister to *Hyles* plus *Xylophanes*. Overall, therefore, the position of *Rhodafra*, together with the related issue of the monophyly of *Hyles*, must still be considered unresolved.

The reconstruction of the proto-*Hyles* (Fig. 10) does not display a combination of characters found in any extant *Hyles* species. The forewings are perhaps most similar to members of the HEC, in that there is a darker (probably olive green-brown) oblique band bounded in black and reduced pattern elements in the costal half of the wing, but with better developed antemedial and postmedial lines. Interestingly, such well-developed lines do occasionally appear in members of the HEC and the closely related *H. dahlii* (e.g., Danner et al. 1998: pl. 32, figs 1, 2), where they could be interpreted as atavistic reversions to the plesiomorphic ground plan condition. The hindwings of the proto-*Hyles* are typical *Hyles*, but there is little variation in the hindwing pattern within the genus and similar patterns are also found in many of the outgroup taxa. The abdominal pattern most closely resembles that of *Hyles euphorbiarum*, but with one fewer pairs of black subdorsal patches. In the broader context of the subtribe Choerocampina, the reconstruction of the proto-*Hyles* does not resemble any other species with the exception of *Rhodafra opheltes*. However, this habitus similarity appears to be another instance of convergent pattern development and expression (Hundsdoerfer and Kitching, in press). Nevertheless, the overall habitus is very *Hyles*-like and we consider it very likely that, were it to be discovered today, such a moth would be described as a species of that genus.

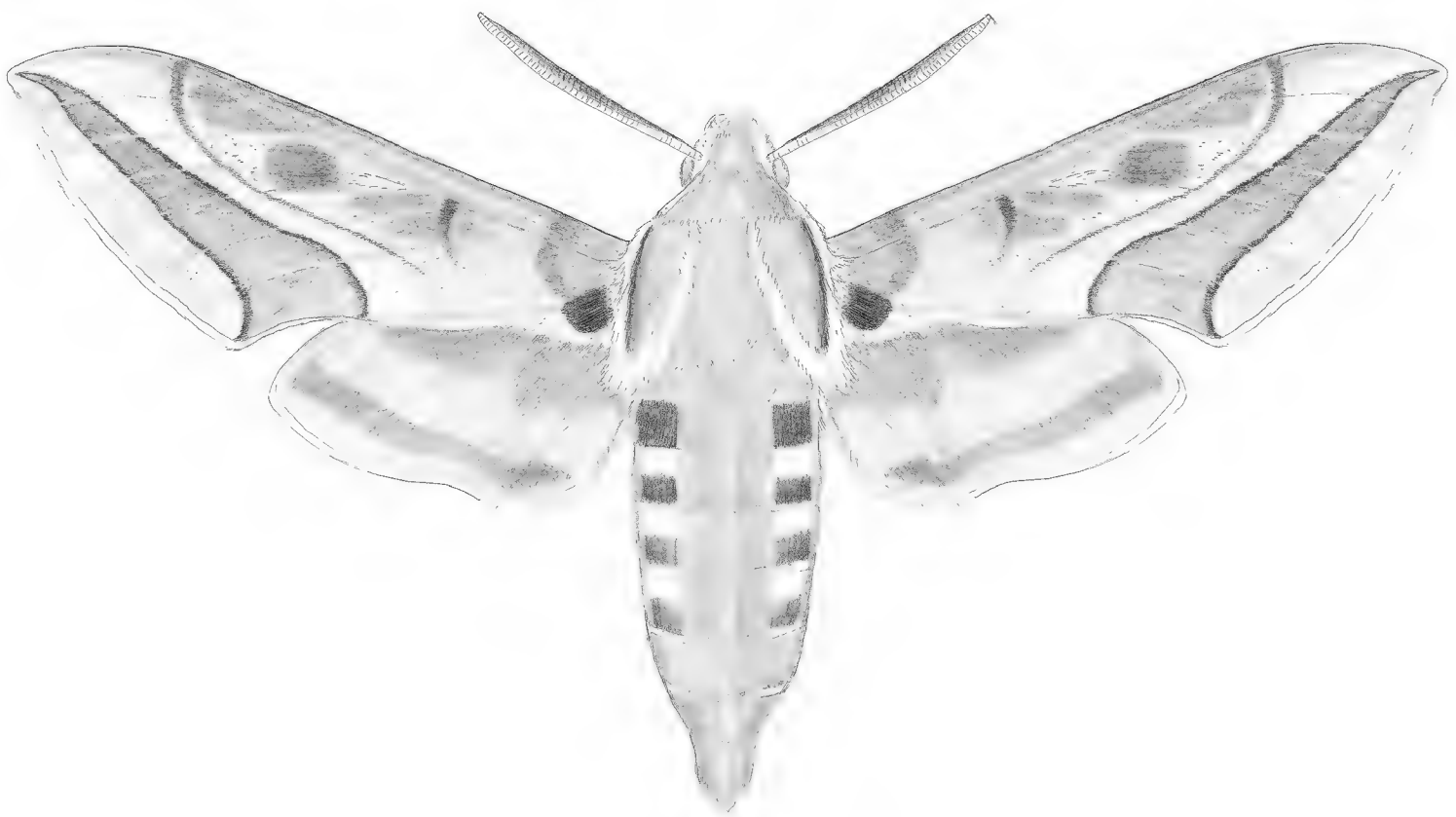

Figure 10. Pencil drawing of the habitus of proto-*Hyles* showing the character states reconstructed (Suppl. material 3: Table S3). The wings were drawn for the right side only and were mirrored for the left side.

Acknowledgements

The EU's Improving Human Potential program SYNTHESYS [grant numbers GB-TAF-3410, GB-TAF-5177] enabled A. K. Hundsdoerfer to undertake collaborative study of morphology of *Hyles* at the Natural History Museum, London, UK. We are particularly grateful to Dr Christian Schmidt for his pencil drawings of morphological structures and to Markward Fischer for their digitisation (both Senckenberg Dresden).

References

Danner F, Eitschberger U, Surholt B (1998) Die Schwärmer der westlichen Palaearktis. Bausteine zu einer Revision (Lepidoptera: Sphingidae). Herbipoliana 4, Verlag Dr. U. Eitschberger, Marktleuthen, 368 pp. (Textband), 720 pp. (Tafelband)

de Freina JJ (1994) Über Biologie, Morphologie und Taxonomie von *Hyles tithymali deserticola* (Bartel), mit vergleichenden Studien zu *Hyles euphorbiae mauretanica* (Staudinger) (Lepidoptera: Sphingidae). Entomologische Zeitschrift 104: 33–60.

Forey PL, Kitching IJ (2000) Experiments in coding multistate characters. In: Scotland R, Pennington RT (Eds), Homology and systematics: coding characters for phylogenetic analysis. Taylor and Francis, London, 54–80.

Goloboff PA, Carpenter JM, Arias JS, Esquivel DRM (2008) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics 24: 758–773. https://doi.org/10.1111/j.1096-0031.2008.00209.x

Hundsdoerfer AK, Kitching IJ (in press) Ancient incomplete inter-generic lineage sorting of *Hyles* and *Rhodafra* (Lepidoptera: Sphingidae). Organisms Diversity and Evolution.

Hundsdoerfer AK, Kitching IJ, Wink M (2005) A molecular phylogeny of the hawkmoth genus *Hyles* (Lepidoptera: Sphingidae, Macroglossinae). Molecular Phylogenetics and Evolution 35(2): 442–458. https://doi.org/10.1016/j.ympev.2005.02.004

Hundsdoerfer AK, Rubinoff D, Attié M, Wink M, Kitching IJ (2009) A revised molecular phylogeny of the globally distributed hawkmoth genus *Hyles* (Lepidoptera: Sphingidae), based on mitochondrial and nuclear DNA sequences. Molecular Phylogenetics and Evolution 52(3): 852–865. https://doi.org/10.1016/j.ympev.2009.05.023

Hundsdoerfer AK, Päckert M, Kehlmaier C, Strutzenberger P, Kitching IJ (2017) Museum archives revisited: Central Asiatic hawkmoths reveal exceptionally high late Pliocene species diversification (Lepidoptera, Sphingidae). Zoologica Scripta 46(5): 552–570. https://doi.org/10.1111/zsc.12235

Hundsdoerfer AK, Lee KM, Kitching IJ, Mutanen M (2019) Genome-wide SNP data reveal an overestimation of species diversity in a group of hawkmoths. Genome Biology and Evolution 11: 2136–2150. https://doi.org/10.1093/gbe/evz113

Kitching IJ (2019) Sphingidae Taxonomic Inventory. Creating a Taxonomic e-Science http://sphingidae.myspecies.info/ [date accessed 17.12.2019]

Kitching IJ, Cadiou JM (2000) Hawkmoths of the world: an annotated and illustrated revisionary checklist. The Natural History Museum & Cornell University Press, London, Ithaca, 227 pp. https://doi.org/10.1111/j.1096-0031.2001.tb00124.x

Maddison WP, Maddison DR (2014) Mesquite: a modular system for evolutionary analysis. Version 2.75. http://www.mesquiteproject.org

Nixon KC (1999–2002) WinClada version 1.0000, published by the author. Ithaca, New York. Formerly available at http://www.cladistics.org [date accessed date accessed 11.08.2004] https://www.winsite.com/Development/Components-Libraries/WinClada

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Rothschild LW, Jordan K (1903) A revision of the lepidopterous family Sphingidae. Novitates Zoologicae 9 (Supplement): 1–972.

Sereno PC (2007) Logical basis for morphological characters in phylogenetics. Cladistics 23: 565–587. https://doi.org/10.1111/j.1096-0031.2007.00161.x

Sharkey MJ, Leathers JW (2001) Majority does not rule, the trouble with majority-rule consensus trees. Cladistics 17: 282–284. https://doi.org/10.1006/clad.2001.0174

Appendix I

Explanation of characters and conventions used in coding the morphological data matrix.

PREAMBLE

- The terms "anterior" and "posterior" refer to the forewing of a moth with its wings conventionally spread (i.e., the wings are not in resting position over the body), such that the costa delimits the anterior margin of the forewing.
- The following gives the equivalents between the terminology adopted here for the transverse lines across the wings and that of Derzhavets (1984) (PM: postmedial; SM: submarginal; M: marginal):
    - PM1+_2 = MU1
    - PM3 = M1
    - PM6 = E
    - SM = Tu
    - M =T

- T1 to T10 refer to tergites 1 to 10 of the abdomen respectively.
- References to the online available colour photographs on the Sphingidae Taxonomic Inventory are included for colour characters.

It should be noted that individual specimens, not species, were coded and so, as a result of individual intraspecific variation, other specimens of the same species may show different states for some characters.

HEAD

1: Dorsal antennal scaling, colour; concolorous along entire length (0) (Fig. 1a) / darker over at least the basal half, compared to distally (1) (Fig. 1b).

The character state "concolorous" generally refers to antennae in *Hyles* that are uniformly white. However, the outgroup taxa and some very dark individuals of *Hyles* can be uniform shades of grey, brown or pink. The antennae of *Hyles lineata* are pale grey basally and so the contrast with the white tip is not as great as in some other species but were still coded as 1. The antennae of some taxa (e.g., *Deilephila elpenor*, *Xylophanes libya*, *X. loelia*) are white for most of their length with only the distalmost ten flagellomeres having darker scaling. These taxa were coded as "0".

2: Labial palp segment 2, lateral hairs protruding through general scaling, presence; absent (0) / present (1) (Fig. 2a–c).

3: Labial palp segment 2, lateral hairs protruding through general scaling, if present, formation into a longitudinal crest; irregular, diffuse band or patch (0) (Fig. 2a) / regular, very dense crest (1) (Fig. 2b, c).

4: Labial palp segment 1, scaling at apex on inner side, regularity; irregular (0) (Fig. 3a) / regular (1) (Fig. 3b).

The form of the apical scaling of the inner side of the labial palp segment 1 was coded from Rothschild and Jordan (1903), confirmed by examination of one specimen from each genus included in the present study. In most genera, the apical scales are hair-like, few in number, irregularly erect and the joint between segments 1 and 2 of the labial palp is visible between them. In contrast, in *Basiothia*, *Hippotion* and *Theretra*, the apical scales are broader and oriented in the same plane as the inner surface of the palp segment as a dense, flat crest, which has an even distal margin and completely obscures the joint between segments 1 and 2 of the labial palps.

LEGS

5: Arolium pad, presence; absent (0) (Fig. 4a) / vestigial (1) (Fig. 4b, c, e, f)/ fully developed (2) (Fig. 4d, g).

A fully developed arolium pad is large (≥ ½ length of the claws) and broadly ovoid. In the vestigial condition, it is small (≤ ⅓ length of the claws) and narrowly ovoid or rectangular (but nonetheless discernible as a distinct structure). When only the base of the arolium is present, and the pad is represented by a minute nipple-like structure or is missing entirely, the arolium pad is coded as absent.

6: Foreleg basitarsus outer row of spines, spines, size and number (compared to other rows); similar in size and number (0) (Fig. 5a, b) / very large and reduced in number (1) (Fig. 5c).

In some specimens, the spines of the outer row are similar in length to the surrounding scales and require careful observation to confirm their presence.

7: Foreleg basitarsus outer supernumerary spines, presence (at least near the base); absent (0) (Fig. 5a) / present at least over basal half (1) (Fig. 5b).

If only one spine is out of line at the base of the basitarsus, this was not considered to be a supernumerary spine. The number of supernumerary spines can vary between the left and right legs of the same individual. Specimens *Hyles centralasiae* 271594, *H. exilis* 251533 and *H. e. euphorbiae* 271762 have no supernumerary spines on the right foreleg but two on the left; they were nevertheless coded as "0".

THORAX

8: Tegula, outer edge, coloration; ground colour (0) (Fig. 6a) / paler (1) (Fig. 6b–f).

The outer edge of the tegula is white or pale buff-coloured, thus strongly contrasting with the darker olive-green or brown scaling of the tegula body, in all taxa except two species of *Xylophanes* and *Hyles vespertilio*.

9: Tegula outer edge, if paler, inner black edge, presence; absent (0) (Fig. 6b–d) / present (1) (Fig. 6a, f).

The amount of black scaling is quite variable, ranging from mere traces, detectable only under stereomicroscopic magnification and requiring the moving apart of other scales to observe (e.g., several *Hyles apocyni* and both subspecies of *H. hippophaes*), to a distinct stripe. Any presence of black was coded as "1".

10: Tegula inner edge, coloration; ground colour (0) (Fig. 6a, c–e) / paler (1) (Fig. 6b, f).

Where the inner edge of the tegula is paler than the ground colour, it is usually white or cream-coloured. In a few specimens (e.g., some *Hyles sammuti*), it has a pinkish tone.

11: Tegula median line, presence; absent (0) (Fig. 6a, b, e, f) / present (1) (Fig. 6c, d).

This line is generally narrow, straight or curved, and is metallic golden-yellow in colour. However, in *Deilephila askoldensis*, it is broader and more diffuse, and in *D. elpenor*, it is additionally dark pink. The median stripe is absent in the pink "form *porcellus*" of *D. porcellus* that was coded here and so this species was coded as "0". However, there is a diffuse dark pink stripe in some specimens of the pinkish-brown "form *rosea*" (e.g., Danner et al. 1998: pl. 39, fig. 21) and a diffuse olive-green stripe is present in some specimens of the brown "form *suellus*" (e.g., Danner et al. 1998: plate 39, fig. 18).

12: Pale thoracic median line, presence; absent (0) (Fig. 6a, b, e, f) / present (1) (Fig. 6c, d).

This line is coded as absent in *Deilephila porcellus*, but this was difficult to determine due to a general blurring of the pattern in this species.

13: Pale thoracic median line, if present, shape; single broad dorsal line (0) (Fig. 6c) / dorsal and median on prothorax, divided either side of the midline on mesothorax leaving a ground colour dorsal line (1) (Fig. 6d).

ABDOMEN

14: Dorsal abdominal line, presence; absent (0) (Fig. 6a, b) / present (1) (Figs. 6c–f, 7a, b).

This line was coded as present even if it was broad and diffuse or reduced to a series of isolated spots on the posterior margins of the tergites. In some specimens, these spots may be merged into a general pale posterior margin to the tergites. Several specimens were coded as "?" because the abdomens were missing (due to genital dissection prior to this study) or worn. The abdomen of the holotype of *Hyles churkini* had been "washed" as part of the genitalia preparation procedure, which removed much of the dorsal scaling; it and the paratype male were coded from pre-dissection colour photographs provided by A. Saldaitis (pers. comm.).

15: Dorsal abdominal line, if present, colour; paler than ground colour of tergites (0) (Figs 6c–f, 7b) / darker than ground colour of tergites (1) (Fig. 7a).

The abdominal line in *Deilephila elpenor* was coded as "0" although it is a darkish pink against an olive-green ground (STI 863). The line was not coded as "1" in *D. askoldensis* as the entire dorsum is only slightly paler and there are clearly pale fringes to the tergites (STI 861).

16: Dorsal abdominal line, if present, form; single (0) (Fig. 6d–f) / double (1) (Fig. 6c).

17: Dorsal abdominal line, if present, form; continuous narrow line (0) (Fig. 6c, d, 7a) / continuous broad diffuse line (1) (Fig. 7b) / continuous broad diffuse line with brighter spots on posterior margins of tergites (2) (Fig. 6f) / represented only by pale spots on tergite margins (3) (Fig. 6e).

Specimens were coded as "3" when the spots form part of a continuous pale posterior fringe to the tergites. In most instances of state "2", the line is visible between all the spots but in some cases (e.g., *Hyles tatsienluica*), the line is visible only on T1 and T2 anteriorly, and T7 and T8 posteriorly. When the line is only vaguely visible on T7/T8 or T8 (e.g., *H. t. tithymali* 271939), or when the dorsal line is essentially ground colour, appearing paler in comparison to more lateral darker areas (e.g., *H. dahlii* 271419), specimens were coded as "3". *Hyles lineata* was coded as "1" as the line is generally continuous and narrow, although on some tergites in some individuals it can be slightly interrupted on the posterior margins (where, also, there are no white spots). In some *H. perkinsi* (e.g., 271628), there is a diffuse band of whitish scales along the dorsum, with a slightly less diffuse patch in the fringes. As there is dark olive brown scaling lateral to this, before the black spots, these specimens were coded as "2". In *H. nervosa* 271553, there are median spots on T5 and T6 only; in others, very weak spots are discernible; all coded as "3". In two others, no spots can be seen. In *H. dahlii* 271424, there is a spot on T3 only (although the other segments are worn). In *H. tithymali mauretanica* 274431, there are a few (maybe < 5) pale scales on the margin of T7 only; this specimen was coded as "0".

18: Median pair of black spots in posterior fringe of tergites of abdominal segments A3-6, presence; absent (0) (Fig. 6a-c, e) / present (1) (Fig. 6d, f).

Careful observation was required when coding characters 18–23 so as not to interpret the dark, heavily sclerotized scales along the edge of the tergites as black top-layer scales. The median pair of black spots is also present on A2 in *Hyles lineata*, *H. livornica* and *H. livornicoides*, but can be difficult to see in pale or greasy specimens, especially in *H. livornicoides*.

19: Black dorso-lateral spot on posterior part of abdominal segment A2, presence; absent (0) (Figs 6c, 7a) / present (1) (Figs 6a, b, d–f, 7b).

The spots are present but very faint in *Deilephila askoldensis*.

20: Black dorso-lateral spot on posterior part of abdominal segment A3, presence; absent (0) (Figs 6c, 7a) / present (1) (Figs 6a, b, d, f, 7b).

21: Black dorso-lateral spot on posterior part of abdominal segment A3, if present, size; A3; covering only a part of the segment, always leaving an anterior area of pale scaling (0) (Figs 6a, b, d, f, 7b) / covering whole segment, no pale scaling (1).

Hyles livornicoides 272011 has a worn abdomen and although the presence of a black spot on A3 can be deduced from the few scales that remain, its extent cannot be determined; hence this specimen was coded as "?".

22: Black dorso-lateral spot on posterior part of abdominal segment A4, presence; absent (0) (Fig. 6b, c, e) / present (1) (Figs 6a, d, f, 7b).

This spot was coded as present even if it is restricted to the fringe of the tergite.

23: Black dorso-lateral spot on posterior part of abdominal segment A4, if present, size A4; covering posterior half of segment (0) (Figs 6a, 7b) / restricted to fringe (1) (Fig. 6f).

In *Hyles nervosa* 271553, this spot is weakly developed (black scales intermixed with some ground colour scales) but still stretches over about half the length of the segment, and so was coded as "1". In the *H. stroehlei* male, the black fringe to A4 is visible; in the female, it would also appear to be present as determined from the pre-dissection photograph.

24: Black dorso-lateral spot on posterior part of abdominal segment A5, presence; absent (0) (Figs 6a–c, e, 7a, b) / present (1) (Fig. 6d, f).

25: Black dorso-lateral spot on posterior part of abdominal segment A6, presence; absent (0) (Figs 6a–e, 7a, b) / present (1) (Fig. 6f).

In *Hyles annei* 271815 and *H. euphorbiarum* 813596, this spot is very small; these were both coded as "1". In *H. annei* 271811 and *H. euphorbiarum* 813551, the spot is a barely visible slightly darker shade; these were coded as "0". In *H. salangensis*, the spots gradually become smaller and fainter from A2 to A6 and are sometimes not visible on the last of these segments. Although often small and faint on A5 and A6, they are still present, resembling in form those on A4 in *H. nervosa* 271553.

26: Dorso-lateral pale scales in fringes of tergites A4-6, presence; absent (0) (Fig. 6a–b, d) / present (1) (Figs 6e, f, 7b).

These scales form a pale cream or white posterior fringe to the tergites in the taxa that have them. In some outgroup taxa, they are restricted to a pair of dorso-lateral spots.

The scales can be short (as in *Hyles livornica* and *H. livornicoides*) or rather long (as in *H. annei*). The spots are present but very faint in *Deilephila elpenor*. In *Hippotion celerio* and *Basiothia charis*, there are smaller silvery-white patches in the fringes that form part of the interrupted dorso-lateral longitudinal stripes. These are considered homologous with the dorso-lateral pale scales in other taxa and so coded as "1". In *B. schenki*, there are white spots in the gold stripe on the fringes on T5 and T6 that are considered homologous the dorso-lateral pale scales in other taxa and so coded as "1".Two *Rhodafra marshalli* have complete paler fringes (pale beige rather than white but were still coded as "1") whereas *R. marshalli* 272081 lacks all pale scales, possibly because it is worn (and so was coded as "?"). In worn *R. opheltes*, the marginal lanceolate scales are somewhat golden and give the impression of a pale fringe; such specimens were coded as "0". In *Hyles lineata* and *H. euphorbiarum*, there are some small white patches in the middle of T3-6 dorso-laterally, but none in the fringes, so these species were coded as "0".

27: Dorso-lateral pale scales in fringes of tergites A4-6, if present, extending towards midline no further than mesal margin of black spots (0) (Fig. 7b) / extending mesad of inner margin of black spots halfway to midline (1) (Fig. 6e, f) / extending across entire width of tergite (2) (STI 1333).

In state 0, the median edges of the black spots and all pale patches and fringes are in line antero-posteriorly, leaving a broad median gap to the pale midline (if present). In some outgroup taxa, the pale scales are restricted to small spots, but these are not mesad of the inner margin of dorso-lateral longitudinal stripes (which occupy the same position as the black patches in other taxa). In state 1, the fringes extend further mesad by a distance about half way to the midline, leaving a narrow gap to the midline (if present). In state 2, the pale fringes are continuous across the entire tergite and include the midline pale spots (if present). In the *Hyles stroehlei* male, the white fringes clearly extend mesad of the inner edge of the black spots on A2 and A3; in the female they do not but this is because the black spots and associated white patches are also extended mesad by the same amount, making the mesal edges of all these elements appear in line. The female was thus coded as "1".

28: Dorso-lateral pale scales in fringes of tergites A4-6, if present, colour; white, cream or pale yellow (0) (Fig. 6e, f; STI 1333) / orange (1) (STI 1352).

In *Hippotion celerio*, there are smaller silvery-white patches in the fringes.

29: Dorso-lateral gold stripe, presence; absent (0) (Fig. 6a, b, d–f, b) / present (1) (Figs 6c, 7a; STI 2856).

FOREWINGS

30: Black basal spot, presence; absent (0) (Figs 8a, 9a) / present (1) (Figs 8b, 9b–d).

The basal spot is spot G of Derzhavets (1994). The base of vein Cu in *Theretra oldenlandiae* has some slightly darker scales but these are brown rather than black and do not constitute a clear spot; this species was coded as "0".

31: Basal band, presence; absent (0) (Figs 8a, 9a) / present (1) (Figs 8b, 9c, d).

The basal band (band F3 of Derzhavets 1994) occupies the basal third of the discal cell and the area posterior to vein Cu (Fig. 8c) as far as the black basal spot (if present). It is darker than the ground colour of the forewing and bounded by the sub-basal line (morphologically the inner edge of the antemedial band). In *Basiothia*, the basal band below the discal cell and above vein 1A + 2A (Fig. 8c) is paler than ground colour rather than darker, whereas the area within the discal cell is ground colour; these species are thus coded as "1".

32: Antemedial band, anterior part in discal cell, presence; absent (0) (Figs 8a, 9a–d) / present (1) (Figs 8b, 9e).

The antemedial band arises from the inner edge and traverses the wing across the discal cell halfway between the subbasal line and the apex of the cell as defined by the origin of vein M_2. Specimens were coded as "-" if the middle of the discal cell and basal part of cell f (see below) are dark, even if the area posterior to cell f is pale and no line is seen; i.e., the antemedial band may exist only within the discal cell to costa (where it is too dark to be seen). A darker crossbar in the discal cell (e.g., in some *Hyles gallii*, notably *H. gallii* 813579) is interpreted as the remains of the antemedial line.

33: Antemedial band, anterior part in discal cell, if present, angle to costa; transverse (0) (Fig. 9e) / oblique (1) (Fig. 9a).

In state 0, the antemedial line curves to run transversely across the discal cell to the costa. In state 1, it runs parallel to the postmedial lines and through the discal spot.

34: Postmedial lines PM1+PM2, presence; absent (0) (Fig. 9b) / present (1) (Figs 8a, b, 9a–f).

Postmedial lines PM1 and PM2 are visible as separate lines in *Hippotion*, *Theretra* and *Xylophanes*. In all other taxa in the present study in which they are discernible, PM1 and PM2 are fused into a single line (see character 35). Specimens are coded as "-" if the basal parts of cells a-b (see below) are dark, even if the area more towards the wing base is pale and no line is seen; i.e., PM1+PM2 may exist only within the basal parts of cells a-b where it forms the "comma mark" (see character 37) (Fig. 9c, d). In other words, this "comma mark" is interpreted as the most distal (and often sole) remnant of PM1+PM2. This character cannot be coded in specimens where the costal stripe is dark (as in *Rhodafra opheltes*, *Hyles euphorbiarum*, *H. zygophylli*, many *H. gallii*, some *H. exilis*), because often only a few dark scales in the costal strip are all there are to indicate the presence of PM1+PM2 apical to vein Rs_4. Where it was unclear whether these few darker scales could be seen as distinct against the background of the costal stripe colour, specimens were coded as "-". PM1+PM2 is interpreted as being present in *H. lineata*, *H. livornica* and *H. livornicoides*, where they are (partly) fused with the dark scaling in cells a-f to give a distinct, apparently truncate border. In most *H. vespertilio*, PM1+PM2 is visible as a slightly darker shade but forms a pattern element that can still interpretable as this line. Most *H. dahlii* have a clear PM1+PM2 but in *H. dahlii* 813555, the general area is filled with a dense scattering of dark scales, obscuring PM1+PM2; hence this specimen was coded as "?". In *H. robertsi elisabethae* 4314, there is a trace of a comma-mark on the right wing but not on the left; however, the moth is worn and so was coded "-". In three specimens of *H. salangensis*, a very faint but complete PM1+PM2 can be seen and these were coded as "1", whereas in the other two, PM1+PM2 cannot be seen and these were coded as "0". However, these two specimens are worn and this may account for the observation.

35: Postmedial lines PM1 and PM2, if present, fusion; not fused (0) (Figs 8a, 9a) / fused (1) (Figs 8b, 9c–f).

Postmedial lines PM1 and PM2 are considered fused if only a single, broad line is visible.

36: Postmedial lines PM1+PM2, if present, direction; running to apex (0) (Figs 8a, 9a) / strongly curving to costa from M1 (1) (Figs 8b, 9c, d).

In state 0, PM1+PM2 do not necessarily have to reach the apex, only run towards it. In state 1, the distal angle of curvature towards the costa is almost 90°.

37: Postmedial lines PM1+PM2, if distally curving to costa beyond M1, development; developed in nearly its entire length, from inner edge to costa (0) (Fig. 9e) / present only distally, i.e. from costa to no further than M2 (1) (Fig. 9c, d).

State 1 is the pattern element commonly referred to as the "comma mark" (Fig. 9c, d). In *Hyles calida*, PM1+PM2 may be stronger between M_1 and costa but still weakly present basal to M_1.

38: Postmedial line PM3, presence; absent (0) (Figs 8b, 9b–f) / present (1) (Figs 8a, 9g).

This line runs within the pale medial band. If PM3 and PM4 are fused (as in *Basiothia schenki*), both are coded as present.

39: Postmedial line PM4, presence; absent (0) (Figs 8b, 9b–f) / present (1) (Figs 8a, 9g).

This line runs within the pale medial band. If PM3 and PM4 are fused (as in *Basiothia schenki*), both are coded as present.

40: Postmedial line PM6, presence; absent (0) (Fig. 9j) / present (1) (Figs 8a, b, 9g).

41: Postmedial line PM5, degree of development; curving costad distal to Rs4 (0) (Fig. 9f) / continuous to wing apex (1) (Figs 8a, b, 9a–c, e, g).

Postmedial line PM5 is present in all specimens studied and so was not coded as a separate presence/absence character. In state 0, PM5 curves towards the costa distal to Rs_4, meeting it nearly at right angles. In state 1, PM5 curves in the opposite direction, running to the wing apex, and generally merging with the apical stripe (Fig. 8A, B, 9A–C, E, G). In *Xylophanes loelia*, PM5 near the costa is represented only by discontinuous series of dark scales; nonetheless, the curvature to the costa can be discerned (Fig. 9g). In *Hyles vespertilio* 813585, PM5 is visible near the inner margin but not across the rest of the wing, hence this character was coded as "?". *Rhodafra marshalli* 272080 is coded as "?" because the wing tips are missing.

42: Postmedial lines PM5 and PM6, relative orientation; subparallel from apex to inner margin (0) (Fig. 9f) / strongly divergent towards inner margin (1) (Figs 8b, 9b, c, e, f).

The critical element of this character is the divergence of the two lines, not the colour between them. In *Rhodafra opheltes* and most *Hyles*, the colour between the divergent PM5 and PM6 is a characteristic olive-green to olive-brown and forms the distinctive triangular postmedial pattern element. PM5 and PM6 are divergent in several other taxa and the colour between the lines varies: *Deilephila elpenor* (khaki), *D. porcellus* (mustard yellow), *D. askoldensis* (pinkish-brown), *Hyles vespertilio* (slightly darker grey with a slight yellowish tinge), *Chaerocina dohertyi* (brown) and *C. jordani* (slightly darker yellowish green).

In *R. marshalli*, PM6 is entirely absent and so is coded as "-" for this character.

43: Postmedial lines PM5 and PM6, coloration between PM5 and PM6; uniform from apex to inner margin (0) (Figs 8a, b, 9a, b) / paler between at least CuA1 and wing apex (1) (Fig. 9d).

In specimens coded as "1", the pale section can extend basally from CuA_1 as far as CuA_2 (in *Hyles perkinsi*, *H. wilsoni* and some *H. n. orientalis*, PM6 is absent distal to CuA_1/CuA_2).

In *R. marshalli*, PM6 is entirely absent and so is coded as "-" for this character.

44: Postmedial line PM5, if present, shape; straight or evenly curved (0) (Figs 8a, b, 9a, b, g) / strongly dentate (1) (STI 1352).

45: Postmedial line PM5, if present, between CuA1 and the inner margin, shape; straight or slightly concave (0) (Figs 8a, 9a, g) / convex towards base (1) (Figs 8b, 9b–f).

This character captures the degree to which PM5 runs straight to the inner margin at an acute angle (Figs 8a, 9a, g) or turns to strike it more nearly at a right angle (Figs 8b, 9b–f). The degree of curvature was estimated by placing a straight edge between the points where PM5 crosses CuA_1 (Fig. 8c) and where it meets the inner margin, and then observing whether any part of PM5 was visible basal to the straight edge. In those taxa with a strongly dentate PM5 line (*Hyles perkinsi*, *H. wilsoni*), the positions of the outer points of the serrations were used to estimate the curvature, ignoring the basally directed points. Even a very slight convexity (as in *Chaerocina jordani*, some *Hyles biguttata* and *Hyles tatsienluica*) was coded as "1". In some specimens (e.g., *Rhodafra opheltes* 813571, *Hyles hippophaes*), the inflection point is not at CuA_1 but at CuA_2 (giving the line a slight S-shape in some *H. hippophaes*), i.e., much closer to the inner wing margin. In these cases, convexity that is limited to the section of the line between CuA_1 and CuA_2 was ignored. In *Rhodafra marshalli*, PM5 in this area is straight along the outer edge and slightly convex along the inner edge, and slightly more so in males than in females; these were coded as "0".

46: Postmedial line PM6, if present, shape between CuA2 and inner margin; straight or slightly convex (0) (Figs 8a, 9a, g) / concave (1) (Figs 8b, 9b–f).

This character was coded using the same protocol as for character 45 but the straight edge is placed between the points where PM5 crosses CuA_2 and where it meets the inner margin.

47: Veins between PM1 and PM6, colour; concolorous with background along whole length (0) (Figs 8a, b, 9a, c, g) / between PM5 and PM6, concolorous with pale medial band (1) (Fig. 9e) / highlighted in white (2) (Fig. 9b).

When the veins are paler, sometimes the bases of the veins can be dark, especially Rs_4. Vein M_2 can be dark due to the presence of very strong spots in cells c and d. *Hyles robertsi elisabethae* 4314 is worn but those scales that are left suggest that the veins are concolorous with the background.

48: Veins across postmedial band, if concolorous with pale medial band, extent; paler at least distally, along a few veins (0) (STI 1339) / paler along at least half of some veins and paler in the position of the middle of the band (1) (Fig. 9e).

49: Postmedial line PM7, presence; absent (0) (Figs 8b, 9b-f) / present (1) (Figs 8a, 9a, g).

This line is often referred to as the submarginal line. Individuals in which PM7 appears to be indicated by a broad, diffuse shade were coded as "0", because this is not a clearly demarcated line. In *Hyles calida*, PM6 appears to fade out into that shade, which makes it difficult to determine, but such specimens were nevertheless coded as "1".

50: Postmedial line PM7, if present, sharpness; distinct line (0) (STI 2856) / indistinctly defined line (1) (STI 1303).

51: Postmedial line PM8, presence; absent (0) (Figs 8b, 9b–f) / present (1) (Figs 8a, 9a, g).

This line is often referred to as the marginal line.

52: Inner margin between PM5 and PM6, fringes, colour relative to area bounded by PM5, CuA_2, PM6 and inner edge of fringes; concolorous (0) (Fig. 9f, g) / entirely paler (1) (Figs 8a, b, 9a–c, e).

53: Line of white scales in basal third of cell between costa and radius, presence; absent (0) (Fig. 9a, c–g) / present (1) (Fig. 9b).

54: Line of white scales in basal half of discal cell, along anterior margin, presence; absent (Fig. 9a–g) (0) / present (1) (STI 1310).

The degree of development of this line of white scales is variable from the wing base to the middle of the cell; if any white scales at all were observed, the specimen was coded as "1".

In *Rhodafra opheltes*, the discal cell basally has a linear patch of cream scales along the posterior margin, the same colour as the pale medial band. As these scales are not white, this species was coded as "0". In *Hyles perkinsi*, and to a lesser extent in *H. wilsoni*, there are scattered white scales over almost the entire wing upperside. However, as this do not form a line, these species were coded as "0".

55: Costal cell ground colour; concolorous with basal band (0) (Fig. 9e, f) / distinctly paler (1) (Figs 8b, 9c, d).

The costal cell is cell K of Derzhavets (1994). In state 1, there is a clearly visible change in the ground colour of the costal cell at the point level with distal edge of the basal band, and the basal section of the costal cell is usually concolorous with the basal band. Care had to be taken to ensure that it was the ground colour of the costal band either side of the subbasal line that was evaluated. The subbasal line itself, when it is visible in this area, is invariably darker than the costal band and this must be ignored. In *Rhodafra opheltes*, the costal cell is very pale basally and gradually becomes darker towards the apex. As it is essentially concolorous in the area in question this species is coded as "0". In the *Hyles tithymali* group, which were coded as "1", the colour difference can be seen although it is very slight and requires careful observation. This area of the forewings in *Hyles robertsi robertsi* 271539 is greasy and discoloured, and so the specimen was coded as "?".

56: Discal cell between subbasal line and apex, colour; entirely dark (0) (Fig. 9a, b, g) / only distal median part pale (1) (Fig. 9e) / entirely pale (2) (Fig. 9c, d).

State 0 is equivalent to the presence of the basal part of spot F2 of Derzhavets (1994).

With regard to coding pale coloration in the discal cell, the area in question extends from the subbasal line distally to the origin of M_2 (Fig. 8C). The small apical triangle bounded distally by the

radius and M_1/M_2 is always dark. Care had to be taken not to mistake any long, white, setose scales for the pale coloration. When present, these scales were lifted or moved aside, and the colour of the scales underneath observed. In addition, dark scaling due to the presence of an antemedial line crossing the cell near its mid-point was also ignored, the colour of the scaling either side of this line being observed. In *Hyles livornicoides*, the discal cell appears pale distally but this is due to the prolongation of the white scale line posterior to the radius in the cell; the species was coded as "0". In state 1 (e.g., *H. exilis*), there is a pale triangle with its narrow base on the area of the discal spot and its point about halfway down the length of the cell. This pale scaling may also be represented by a more amorphous paler patch that extends within the discal cell, towards the subbasal line (e.g., *H. annei* 271806). In the holotype of *H. churkini*, this patch is a fawn colour, rather than cream-buff. In state 2, both the posterior edge and median part of discal cell are pale. The pale coloration can extend as far as anterior edge of discal cell, but often does not. In *H. euphorbiarum* and *Rhodafra opheltes*, only the posterior edge of discal cell is pale, the central area being entirely dark; both these species were thus coded as "0". In species such as *Hyles biguttata*, where the wing is relatively dark overall, care had to be taken to compare the shade within the discal cell with the overall ground colour. This character cannot be coded in *H. vespertilio* (Fig. 9f) because there is no reference point to compare the colours with the PM band or spots; this species was coded as "?". In some specimens of the *H. tithymali* group, there are extensive long white scales in the cell. If the inside anterior edge, and particularly the inside posterior edge, of the discal cell is dark, and there are no obvious normal broad pale scales, then the specimen was coded as "0". *H. t. deserticola* 813557 is very pale but the inner leading and trailing edges of the discal cell are the same shade as the costal cell and cells a and b, and darker than the pale medial band, and thus it was coded as "0". *H. t. gecki* 272252 has a similar appearance to *Hyles exilis*, in that, when the long white scales were ignored, there is a clear triangular area of normal broad pale scales; this specimen was thus coded as "1".

57: Scaling in cell a (Fig. 8b), presence of dark shading of a similar colour and tone to the area between PM5 and PM6; absent (0) (Figs 8a, 9a, c, d, g, h) / present (1) (Figs 8b, 9b, e).

This is the distal part of spot F1 of Derzhavets (1994) and is in cell Rs_3-Rs_4 (Fig. 8C). Generally, the dark scaling is only present in the basal part of the cell (in the angle between Rs_3 and Rs_4) but can extend distally to a varying extent. In *Hyles vespertilio*, the forewing is almost uniformly grey. However, although the colour in cell a (Fig. 8B) and the area between PM5 and PM6 is concolorous, this is not the feature that is being coded in this character and so the species was coded as "?". The same argument also applies to characters 60-64 and those that are contingent upon them. Care had to be taken not to code the presence of PM1+2 (the "comma mark") in the basal part of cell a (e.g., *H. calida*, *H. nicaea*) as the presence of darker shading in the context of the present character. In *H. annei*, cells a and b (character 60) are slightly darker but this is due to suffusion (character 65), as in *H. biguttata*, and it is not the same colour as between PM5 and PM6; this species was thus coded as "0",

58: Scaling in cell b (Fig. 8b), presence of dark shading of a similar colour and tone to the area between PM5 and PM6; absent (0) (Figs 8b, 9a, c, d, g, h) / present (1) (Fig. 9b, e).

This is the basal part of spot F1 of Derzhavets (1994) and is in cell Rs_4-M_1 (Fig. 8c). The dark scaling appears first at the base of the cell and can then extend distally to a varying extent. The

presence of PM1+2 ("comma mark") in the middle part of cell b (e.g., *Hyles calida*, *H. nicaea*) was not coded as presence of this darker shading. In several *H. nicaea lathyrus* (India 12, 14, 15), the darker scaling in this cell is reduced to a few, very small patches.

59: Scaling in cell c (Fig. 8a), presence of dark shading of a similar colour and tone to the area between PM5 and PM6; absent (0) (Figs 8a, 9a, h) / present (1) (Fig. 9b–e).

This is the distal part of spot D of Derzhavets (1994) and is in cell M_1-M_2 (Fig. 8c). The dark scaling appears first at the base of the cell and can then extend distally to a varying extent. Care had to be taken not to use the pale cream line highlighting the area immediately anterior of PM5 (as in some *Hyles calida*, *H. annei* and *H. biguttata*) as a comparison. In *Hyles siehei* 271581, there is a darker pink patch in cell d but as it is not concolorous with the area between PM5 and PM6, this specimen was coded as "0". In *Hyles apocyni* MTD TW 4535, there are very small patches in both cell c and cell d (character 60); the specimen was coded as "1" for both characters.

60: Scaling in cell d (Fig. 8b), presence of dark shading of a similar colour and tone to the area between PM5 and PM6; absent (0) (Figs 8a, 9a, g) / present (1) (Fig. 9b–i).

This is the antero-distal part of spot D of Derzhavets (1994) and is in cell M_2-M_3 (Fig. 8c). The dark scaling appears first on the border with cell c and/or at the base of the cell and can then extend distally to a varying extent. Characters 60-64 cannot be coded in *H. vespertilio* (Fig. 9f; cf. notes to characters 56 & 57).

61: Scaling in cells e & f (Fig. 8b), presence of dark shading of a similar colour and tone to the area between PM5 and PM6; absent (0) (Figs 8a, 9a, g) / present (1) (Fig. 9b, i).

These are the antero-distal and postero-distal parts of spot F2 of Derzhavets (1994) and are in cells M_3-CuA_1 and cell CuA_1-CuA_2 (Fig. 8C) respectively. They always co-occur and were thus treated together in a single character. Care had to be taken not to code the presence of an antemedial band or PM1+2 in the middle part of cell e (as in *Hyles perkinsi*) as the presence of darker shading in the context of the present character. Likewise, any long white hairs were ignored. The dark scaling in cells e and f is very scant in all *H. euphorbiarum* and often obscured by overlying long white scales; nevertheless, these specimens were coded as "1".

H. dahlii 813555 is a generally dark moth but although there are darker scales in cells e and f, they are not the same colour as the area between PM5 and PM6; hence this specimen was coded as "0".

62: Suffusion in the median area between PM2 and PM5 and M1 and CuA1 (Fig. 8), presence; absent (0) (Figs 8a, 9a, g) / present (1) (Fig. 9h).

This suffusion is a wash of darker scales extending from the costa towards PM5 along the entire length of the wing, parallel to the costa. In *Hyles*, it usually results in the cream colour of the medial band becoming restricted to a narrow band along the basal edge of PM5 (e.g., *H. annei*, *H. biguttata*, *H. calida*). It is usually broader towards the inner margin of the wing and may even reach PM5 on the inner edge of the wing. Care had to be taken when coding pale specimens (mostly populations from arid or semi-arid habitats; e.g., *H. nicaea orientalis*), in which the suffusion may not be very dark. In state 0, there may be suffusion as far as PM2. This was not coded as presence

because of observational difficulties in very spotty moths. If the wing is uniformly darker, this character is coded as "0" (e.g., *H. wilsoni*, *H. perkinsi*, *H. vespertilio*, some *H. nicaea*). In *H. gallii* MTD TW 4367, a particularly dark specimen, there is a slight suffusion between M_3 and CuA_1 only; this is coded as "0".

There is a similar wash of darker scaling in *Deilephila porcellus*, *D. elpenor* and *D. askoldensis* 813599. These species were also coded as "1". The general grey coloration in *Hyles vespertilio* is not interpreted as a suffusion and this species is coded as "?". It is unclear whether the pattern in *H. perkinsi* and *H. wilsoni* involves a suffusion or not, and thus these are also coded as "?". This area in *H. nicaea lathyrus* is heavily patterned with transverse striae but if these are ignored, then there is no suffusion. The gap between PM2 and PM5 in *H. dahlii* is very narrow but contains no suffusion. In *H. t. tithymali* 271939, there is some suffusion between M_3 and CuA_2, which is coded as "1".

63: Dark shading of a similar colour and tone to the area between PM5 and PM6 in cells c and d, if present, apical shape; extending apically and filling width of both cells c and d (0) (Fig. 9b) / apically rounded in each cell separately, appearing bilobed (1) (STI 1301) / apically convergent to form a single rounded, oval or elongate element (2) (Fig. 9c-e).

This character codes for the shape of spot D of Derzhavets (1994). Specimens were coded as "-" if the shading was absent from either or both cells c and d. The condition in which the dark shading in both cells is apically rounded (state 1; e.g., *Hyles euphorbiarum*) is easily recognizable. However, care had to be taken when coding the other two states, particularly with regard to cell c, in which either dark scales extend distally towards the position of PM1+2 and fill or nearly fill that area (state 0; e.g., *H. lineata*, *H. livornica*, *H. t. tithymali*), or the anterior-distal triangle of cell c is entirely pale (state 2; e.g., *H. euphorbiae*, *H. nicaea*, *H. t. mauretanica*). In the first case, there may also be long hair-like white scales overlying the dark scales that fill the anterior-distal triangle, giving the impression that the apex of the dark shading in cell c is rounded, and thus superficially resembling the condition coded for by state 2. These long white scales were ignored for the purposes of coding the present character. In some *Hyles nicaea* (e.g., *H. n. nicaea* 813544, *H. n. castissima* 813547, *H. n. orientalis* 271670 and *H. n. orientalis* 271666), the element in cell c is slightly divided apically, but these specimens were nevertheless coded as "2". In *Deilephila askoldensis*, the rounded shape consists of dark scaling in cells b, c and d, but since the shape resembles the rounded element of cells c and d in *Hyles* species, *Deilephila askoldensis* was nevertheless coded as "1". In *Hyles biguttata* 271823, the apex of the c-d spot is rather pale, giving the impression of state 1. However, the two spots are not as elongate as in those species with state 1 but are short as in species with state 2. In addition, the wings are worn and much of the pattern is less clear. Hence this specimen was coded as "2". *Hyles zygophylli* is difficult to code as several specimens are apparently intermediate between states 1 and 2; they were coded as the state that they more closely resembled. Some *H. nervosa* (e.g., 271553) have a strongly developed PM1 +PM2 in cell c, which gives the impression that the dark pattern element reaches that far. However, this does not match the pattern coded as "1" in *H. livornica* and if PM1+PM2 is ignored, then these *H. nervosa* specimens are clearly state "2".

64: Long hair-like scales on the inner wing margin near wing base, immediately distal to basal spot, colour; ground colour only (0) (Fig. 9a, g) / white, at least at their tips (1) (Fig. 9b, i).

65: Additional long, hair-like scales, presence; absent (0) / present (1).

These long, hair-like scales are usually white, but they can be ground colour (e.g., *Hyles centralasiae* 271585, 271593, *H. sammuti*). They are additional to those scales coded in the previous character.

66: Anterior-distal triangle in cell c, if dark, apparent colour; as dark as rest of element (0) (STI 1310) / with overlying long pale hair-like scales that make it appear pale (1) (Fig. 9b, STI 1312).

In state 0, the anterior-distal triangle is as dark as the rest of the element more basal to it in the cell, and thus almost or completely reaches PM1+2. In state 1, this triangle is also dark but there are long, pale (usually white) scales overlying it that give the superficial impression that it is pale and thus appearing to obliquely truncate the element and superficially resemble state 2 of character 63. For taxa with states 1 or 2 for that character, character 66 is coded as "-".

67: Longish white scales in distal half of discal cell, presence; absent (0) / present surrounding or immediately basal of the position of discal spot (1).

The degree of development towards the centre of the discal cell is variable. *Hyles robertsi elisabethae* 4314 was coded as "?" because the general degree of wear suggests that any white scales that may have been present have been lost. In *H. nicaea castissima*, the white scales are present but are difficult to observe against the general very pale beige ground colour. In *H. siehei*, some *H. centralasiae*, and *H. e. euphorbiae* 813554, the scales are present but beige or pinkish, rather than the usual white; these specimens were nevertheless coded as "1".

68: Discal spot, presence; absent (0) (Fig. 9d, f) / present (1) (Fig. 9a–c, e, g, h).

The discal spot is situated just distal of the discal cell, posterior to vein M_2. The apparently pale discal spots in *Hyles vespertilio* and *H. perkinsi* are due to long white scales at the apex of the discal cell and are not homologous with other white discal spots (e.g., *Deilephila elpenor*). These two species were thus coded as "0".

69: Discal spot, if present, colour; dark (0) (Fig. 9a–c) / pale (1) (STI 863).

The colour of the discal spot in *Hyles euphorbiarum* is difficult to code because it is strongly reflective, the effect of which is to make it appear paler. However, the scales are darker than those surrounding them, and hence this species was coded as "0".

HINDWINGS

70: Marginal band, colour compared to submarginal band; concolorous (0) (Fig. 9f) / slightly paler, border between the two bands diffuse (1) (Fig. 9a, g) / clearly paler, border between the two bands distinct (2) (Fig. 9b–e, h).

This character was difficult to code in *Deilephila elpenor* because the medial and marginal bands are both pale pink and the submarginal band is only slightly darker pink. It was also difficult to code in *D. askoldensis* and *Chaerocina jordani* because the submarginal band is poorly developed (appearing only as a slight dark line distal of about M_3). In *Hyles siehei* 271581, the submarginal band is a very broad pink shade. This specimen was coded as "2" because in *H. sammuti* 271694, there is a narrower shade of the same colour that was also coded as "2". In *H. gallii* 4366, the marginal band between CuA_2 and 1A+2A is paler with a distinct inner margin, whereas distal to CuA_2 the marginal band absent (or at least very indistinct); nevertheless, this specimen was coded

as "2". In *Hyles siehei* ab. *privata*, the black submarginal band is absent and so this character and the two relating to its basal prolongations are all coded as "?".

71: Medial band, distinct cream or white spot on inner margin, presence; absent (0) (Fig. 9a, g) / present (1) (Fig. 9b–f, h, i).

The pale spot has to be distinctly differentially coloured from the medial band and has to be on the inner margin. It is faint in *Hyles vespertilio* but present. In *Xylophanes tersa*, the whole medial band is primrose yellow; in *X. loelia*, the inner margin is beige; in *Basiothia charis*, the inner margin is concolorous with the medial area but there is a small beige patch near the tornus. All these species were coded as "0". In *Hyles lineata*, the pink/white scales of the anal area of the hindwing are relatively sparse and seem to be easily lost, whence the white under-layer becomes prominent. Such specimens were coded as "0".

72: Medial band, colour intensity; concolorous between Rs and CuP (0) (STI 1320) / medial band between Rs and CuA_2 distinctly paler than between CuA_2 and CuP (1) (STI 1303). The disjunction in colour intensity has to be abrupt to be coded as "1". If the medial band only gradually becomes paler towards to costa then it is coded as "0".

73: Inner edge of submarginal band, prolongation towards base along veins, presence; absent (0) (STI 1303) / present (1) (STI 1344 from Madeira).

Such prolongations are only coded as "1" if they are clearly and regularly present along at least M_1 to CuA_2 (Fig. 8c). Specimens in which there are only very short and thin lines along a few veins, often on only one wing (as in *Hyles nicaea lathyrus* 271661), were coded as "0". The submarginal band in *Deilephila elpenor* is a slightly darker shade of pink compared to the medial band; nevertheless, it is possible to code the shape of the inner edge. Three of five *Hyles wilsoni* have no clear prolongation along the veins, although the veins do have some scattered black scales that could be interpreted as the same feature. However, as they do not form a clear pattern element, these specimens were coded as "0".

74: Inner edge of submarginal band, prolongation towards base between each of veins M_1 and CuA_2, presence; absent (0) (Fig. 9g) / present (1) (STI 1282).

As for character 76, such prolongations are only coded as "1" if they are clearly and regularly present between all five veins. Specimens in which there are one or two short prolongations between two or three of the veins, often on one wing only (as in some *Hyles wilsoni*) were coded as "0".

75: Underside, black tornal spot, presence; absent (0) (STI 1350) / present (1) (STI 1303).

Care had to be taken not to code elements of the dorsal wing pattern that show through to the underside. To be coded as "1", there must be a distinct spot. In *Hyles apocyni* SMTD MTD TW 4537 and *H. hippophaes hippophaes* 813567, there are only a few scattered scales in this area of the wing that do not coalesce into a distinct spot; these specimens were coded as "0". In some *H. nicaea*, there is a series of closely spaced brown striae arranged into a patch as large as in other *Hyles* that are coded as having a tornal patch. Although these appear to be the same structures that form the darker patch in other *Hyles*, they do not coalesce into a uniformly dense patch and so were coded as "0". In *H. nicaea nicaea* 813544 and *H. nicaea nicaea* 813545, however, there is such a coalescence and these specimens were coded as "1".

References:

Danner F, Eitschberger U, Surholt B (1998) Die Schwärmer der westlichen Palaearktis. Bausteine zu einer Revision (Lepidoptera: Sphingidae). Herbipoliana 4: 1–368 (Textband), 1–720 (Tafelband).

Derzhavets YA (1994) Phylogenetic interrelations of the sphinx moths of the genus *Hyles* Hbn. (Lepidoptera, Sphingidae). Entomological Review 73: 34–52.

Rothschild LW and Jordan K (1903) A revision of the lepidopterous family Sphingidae. Novitates Zoologicae 9 (supplement): cxxxv + 1–972.

Supplementary material 1

Table S1

Authors: Anna K. Hundsdoerfer, Ian J. Kitching

Data type: matrix of characters and character states

Explanation note: Matrix of 75 characters and character states derived from the external morphology of 218 Choerocampina individuals, with a focus on the genus *Hyles*.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/nl.43.49512.suppl1

Supplementary material 2

Table S2

Authors: Anna K. Hundsdoerfer, Ian J. Kitching

Data type: label data

Explanation note: Locality and other label data for the specimens coded in Table S1.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/nl.43.49512.suppl2

Supplementary material 3

Table S3

Authors: Anna K. Hundsdoerfer, Ian J. Kitching

Data type: species characters and character states

Explanation note: Character states analysed for the ancestral state reconstruction and the suite of inferred states used to produce the illustration of the proto-*Hyles* moth shown in Fig 10.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/nl.43.49512.suppl3

Supplementary material 4

Figure S1

Authors: Anna K. Hundsdoerfer, Ian J. Kitching

Data type: figure

Explanation note: (**a**) Strict consensus tree (SCT) of the 82166 MPCs of length 432 steps found by analysis of the 75 morphological characters under EW. (**b**) 50% majority rule consensus tree (MRCT) of the 82166 MPCs of length 432 steps found by analysis of the 75 morphological characters under EW.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/nl.43.49512.suppl4

Supplementary material 5

Figure S2

Authors: Anna K. Hundsdoerfer, Ian J. Kitching

Data type: figure

Explanation note: Strict consensus tree of the 37 most parsimonious (fittest) cladograms found by analysis of the 75 morphological characters under implied weighting (IW) (K = 16).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/nl.43.49512.suppl5